U.S. Department
of Commerce

Volume 112
Number 1
January 2014

Fishery Bulletin

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The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

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For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Subscription price per year: $32.00 domestic and $44.80 foreign. Cost per single issue: $19.00 domestic and $26.60 foreign. **See back for order form.**

Fishery Bulletin

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The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. It began as the Bulletin of the United States Fish Commission in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the *Fishery Bulletin* of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

U.S. Department of Commerce
Seattle, Washington

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Strandings as indicators of marine mammal biodiversity and human interactions off the coast of North Carolina

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Abstract—The adjacency of 2 marine biogeographic regions off Cape Hatteras, North Carolina (NC), and the proximity of the Gulf Stream result in a high biodiversity of species from northern and southern provinces and from coastal and pelagic habitats. We examined spatiotemporal patterns of marine mammal strandings and evidence of human interaction for these strandings along NC shorelines and evaluated whether the spatiotemporal patterns and species diversity of the stranded animals reflected published records of populations in NC waters. During the period of 1997–2008, 1847 stranded animals were documented from 1777 reported events. These animals represented 9 families and 34 species that ranged from tropical delphinids to pagophilic seals. This biodiversity is higher than levels observed in other regions. Most strandings were of coastal bottlenose dolphins (*Tursiops truncatus*) (56%), harbor porpoises (*Phocoena phocoena*) (14%), and harbor seals (*Phoca vitulina*) (4%). Overall, strandings of northern species peaked in spring. Bottlenose dolphin strandings peaked in spring and fall. Almost half of the strandings, including southern delphinids, occurred north of Cape Hatteras, on only 30% of NC's coastline. Most stranded animals that were positive for human interaction showed evidence of having been entangled in fishing gear, particularly bottlenose dolphins, harbor porpoises, short-finned pilot whales (*Globicephala macrorhynchus*), harbor seals, and humpback whales (*Megaptera novaeangliae*). Spatiotemporal patterns of bottlenose dolphin strandings were similar to ocean gillnet fishing effort. Biodiversity of the animals stranded on the beaches reflected biodiversity in the waters off NC, albeit not always proportional to the relative abundance of species (e.g., *Kogia* species). Changes in the spatiotemporal patterns of strandings can serve as indicators of underlying changes due to anthropogenic or naturally occurring events in the source populations.

Manuscript submitted 8 February 2013.
Manuscript accepted 1 November 2013.
Fish. Bull. 112:1–23 (2014).
doi: 10.7755/FB.112.1.1

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necesarily reflect the position of the National Marine Fisheries Service, NOAA.

Marine biogeographic boundaries are remarkable 1) for the diversity of species that occur as a result of the biogeographically distinct provinces on either side of the environmental or dispersal discontinuities (e.g., Ekman, 1953; Searles, 1984) and 2) for the long-term influences of these boundaries on phylogeography (e.g., Wares et al., 2001; Adams and Rosel, 2006). Several marine biogeographic boundaries occur along the continental United States, such as at Point Conception, California; Cape Canaveral, Florida; Cape Cod, Massachusetts; and Cape Hatteras, North Carolina (NC) (Briggs, 1974; Fautin et al., 2010). The faunal transition zone at Cape Hatteras results from the juxtaposition of warm waters from the northeast-flowing Gulf Stream and cool waters from the south-flowing Virginia Current and leads to the occurrence of both temperate and subtropical-tropical species of algae (Searles, 1984), invertebrates (Cerame-Vivas and Gray, 1966; Baker et al., 2008), ichthyoplankton (Grothues and Cowen, 1999), and fishes (Schwartz, 1989) along the NC coast. In addition to the biogeographic boundary at Cape Hatteras, the Cape is the closest point of land to the Gulf Stream along the mid-Atlantic coast (Briggs, 1974), concentrating pelagic fauna relatively close to shore. Many fish species occurring in NC waters are estuarine-dependent coastal migratory species from northern and southern biogeographic provinces (Ray et al., 1997), taking advantage of NC estuaries, the second largest estuary system in the continental United States (Paerl et al., 2001).

The conditions described previously create an environment conducive for productive commercial (Steve et al., 2001) and recreational fisheries

(NCDMF[1]). Commercial fishing gear, such as gill nets that entangle the endangered North Atlantic right whale (*Eubalaena glacialis*; hereafter 'right whale') (Kraus et al., 2005) and the common bottlenose dolphin (*Tursiops truncatus*; hereafter 'bottlenose dolphin') in NC waters (Byrd et al., 2008), and longlines that entangle pilot whales (*Globicephala* spp.) and Risso's dolphins (*Grampus griseus*) (Garrison, 2007) pose risks for marine mammals. These risks, along with 2 major shipping ports and an active boating and recreational fishing community, intersect with a presumed high diversity of marine mammals along the NC coast.

Documenting and monitoring the biogeographic stratification and biodiversity of marine mammals often requires large-scale aerial or shipboard surveys (e.g., Mullin and Fulling, 2003; Torres et al., 2005). Another mechanism for determining species presence, and potentially relative abundance, is the monitoring of stranded animals over time, especially when monitoring can be conducted in a systematic way (Evans and Hammond, 2004; Pyenson, 2011). Marine mammal strandings (hereafter 'strandings') provide researchers with rare access to protected species and serve as an invaluable source of information on their spatiotemporal distribution (e.g., Maldini et al., 2005; Nemiroff et al., 2010), and biology (e.g., Fernandez and Hohn, 1998; Thayer et al., 2003; Gannon and Waples, 2004). In addition, stranding investigations have been critical in documenting human-induced serious injuries and mortality, such as from vessel strikes (e.g., Campbell-Malone et al., 2008), fishery entanglements (e.g., Byrd et al., 2008; Cassoff et al., 2011), and sonar effects (e.g., Jepson et al., 2005). Changes in temporal or spatial patterns of strandings may serve as indicators of underlying changes in the source populations that were driven either by human causes (see previous references in this paragraph) or by naturally occurring events (e.g., Evans et al., 2005; Johnston et al., 2012; Peltier et al., 2013).

We examined spatiotemporal patterns of marine mammal strandings in NC over a 12-yr period when stranding response effort was relatively consistent and high and examined whether those observed patterns, and patterns of species diversity, reflected published records of marine mammal populations off the NC coast. While in waters off NC, marine mammals are at risk of interactions with commercial fisheries; therefore, patterns of human interactions evident from strandings were also evaluated. This study is the first comprehensive overview of NC stranding records.

Materials and methods

North Carolina geography

North Carolina's ocean coastline (~537 km) (Fig. 1) is a series of barrier islands separated from the mainland by various sounds and the Intracoastal Waterway. Several state and federal parks and reserves (>227 km) occur on the barrier islands, some of which are accessible only by boat. In addition, property at the U.S. Marine Corps base at Camp Lejeune is off-limits to unauthorized personnel—an area that includes the inshore (defined here as inside the International Regulations for Preventing Collisions at Sea [COLREGS] demarcation line[2]) coastline at the base, Brown's Island (~8 km long), and Onslow Beach (~18 km long). All inshore coastline poses significant challenges for detection of and responses to stranded animals; the expansive estuary system has many remote areas and much of the shoreline consists of cordgrass (*Spartina* spp.) where carcasses may not be detected.

Stranding response and data collection

Although responses to strandings occurred intermittently in NC as early as the mid-1970s (Mead[3]), coverage by an extensive stranding network has been most consistent since 1997. From February 1997 through February 1998, researchers at the National Marine Fisheries Service, Beaufort Laboratory in NC (hereafter 'NMFS-Beaufort') led a systematic, intensive, statewide effort to document strandings that may have resulted from interactions with fisheries. Surveys were conducted weekly by driving the same route along ocean-side beaches. During that year, the network was expanded and strengthened to ensure that reporting of strandings would continue after conclusion of the project. From 1998 through 2008 the network continued a collaborative stranding response with multiple agencies in the state. In 2008 the NC stranding network underwent reorganization; therefore, only data from

[1] NCDMF (North Carolina Division of Marine Fisheries). 2012. North Carolina License and Statistics Section summary statistics of License and Permit Program, Commercial Trip Ticket Program, NC Marine Recreational Information Program, Striped Bass Creel Survey in the Central and Southern Management Area, NC Recreational Saltwater Activity Mail Survey, 399 p. [Available from NCDMF, 3441 Arendell St., Morehead City, NC 28557 or http://portal.ncdenr.org/c/document_library/get_file?uuid=6cd202a9-45e6-4e42-bb83-418ead9db653&groupId=38337, accessed June 2013.]

[2] The line of demarcation delineating waters upon which mariners shall comply with the International Regulations for Preventing Collisions at Sea, 1972, and those waters upon which mariners must comply with the Inland Navigation Rules as described in 33 CFR part 80. [Available from http://www.gpo.gov/fdsys/pkg/CFR-2012-title33-vol1/pdf/CFR-2012-title33-vol1-part80.pdf, accessed November 2013.]

[3] Mead, J. G. 1979. An analysis of cetacean strandings along the eastern coast of the United States. *In* Biology of marine mammals: insights through strandings (J. B. Geraci and J. St. Aubin, eds.), p. 54–68. Final report to the U.S. Marine Mammal Commission in fulfillment of Contract MM7AC020. Report Number PB-293890. [Available from the U.S. Marine Mammal Commission, 1625 I St., NW, Washington, D.C. 20006.]

1997 through 2008 were examined here. During those years, the state was divided into 2 primary response areas with overlap as needed. Responders from NMFS-Beaufort covered mainly the area north of New River Inlet to the NC–Virginia (VA) border, whereas responders from the University of North Carolina Wilmington covered predominantly south of New River Inlet to the NC–South Carolina (SC) border (Fig. 1). Strandings were reported by means of a dedicated phone number or 24-hour pager, and came from a variety of sources, including the public, local municipalities, and state and federal agencies. Generally, public reporting was opportunistic. Some areas and seasons, however, had more systematic coverage. For example, participants of the NC Sea Turtle Project reported strandings observed during daily surveys of ocean beaches for sea turtle nests. These surveys occurred each year from May 1 through August 31 and were almost state-wide, including Onslow Beach. The only exceptions were 2 barrier islands accessible only by boat (totaling ~20 km) that were surveyed only twice per week and Brown's Island, which was not surveyed because of live-fire exercises conducted by the U.S. Marine Corps. Outside of the sea turtle nesting season, national and state park rangers conducted weekly surveys within state and federal parks.

Figure 1

(**Upper left**) Coast of North Carolina (NC) showing major bodies of water, landmarks, and bathymetry. The black boundary line around New River represents Camp Lejeune, property of the United States Marine Corps. (**Lower right**) Stratification of coastal beaches for spatial analysis by segment from the Virginia–NC border south to the NC–South Carolina (SC) border: north of Cape Hatteras (A1–A2), Cape Hatteras to Cape Lookout (B1–B2), Cape Lookout to Cape Fear (C1–C2), and Cape Fear to SC (D).

Marine mammals were considered stranded if they were dead (either on land or in the water) or alive and in need of human intervention (e.g., cetaceans stranded on land, marine mammals entangled in fishing gear, sick or injured seals, seals that were relocated to a more secluded location due to human and animal welfare concerns). For each stranding, standard data (level A) (e.g., species, geographic coordinates, length, sex) and additional data (e.g., extensive morphometrics, life history) were collected when possible according to protocols reviewed in Geraci and Lounsbury (2005). Common and species names were taken from the list published by the Society for Marine Mammalogy [http://www.marinemammalscience.org]. Various samples were collected systematically (e.g., for genetic analysis or *ad libitum* (e.g., for histological, toxicological analysis) for sample banks or for further biological studies.

Each stranding was assigned a human interaction (HI) category: yes, no, or could not be determined (CBD) (Read and Murray, 2000). Strandings were classified as HI-CBD if 1) the carcass was too decomposed to determine presence or absence of HI evidence, 2) the carcass was not examined for HI evidence, 3) the required information was not recorded, or 4) suspicious lesions could not be identified definitively as HI. A description of HI evidence was recorded for most HI-yes strandings, although recognizing that the interaction may not have caused the mortality. HI-yes strandings were further stratified by HI-FI (fishery interaction) (e.g., evidence of entanglement lesions, including healed lesions, or gear present) or HI-other (e.g., mutilations, propeller wounds, vessel strikes, gunshots, debris ingestion) (Byrd et al., 2008). Animals positive

for FI with additional HI evidence were categorized as HI-FI with other evidence noted. Mutilation was distinguished from scavenger damage according to guidelines in Read and Murray (2000). In contrast to the consistent definitions of HI described above, the HI-other designation due to human harassment of live pinnipeds and cetaceans on the beach was applied inconsistently by stranding responders through the years because it is not clearly defined by the NMFS Marine Mammal Health and Stranding Response Program (MMHSRP), although such cases arguably fit the definition of harassment under the Marine Mammal Protection Act (MMPA; Title 16, U.S code [USC] 1361). Live seals are particularly vulnerable to harassment, especially in NC where their presence on the beach is relatively novel. As a result, each record of a live seal stranding was reviewed during the compilation of stranding data for this study. Seals not otherwise in need of medical attention (i.e., stranded) were considered stranded and classified as HI-other when a high level of harassment occurred (e.g., when they were touched by humans or relocated because of repeated disturbance), but not when seals were frightened back into the water. Live stranded cetaceans that the public pushed back into the water before notifying stranding responders were not generally classified as HI-other (i.e., harassed) according to the Southeast Regional MMHSRP policies.

Whenever possible, genetic analysis was conducted to verify or assign species identification for animals not identified to species in the field owing to advanced decomposition and for species hard to identify (e.g., *Kogia*, *Stenella* species). Genetic analysis also was used to assign the coastal or offshore morphotype (Rosel et al., 2009) for 185 samples from bottlenose dolphins. All other bottlenose dolphins were by default considered the coastal morphotype.

Stranding data and analyses

Stranding data from January 1997 through December 2008 were compiled from the comprehensive database maintained at NMFS-Beaufort. Level A stranding data from NC are also maintained in the MMHSRP database; however, the local database includes additional data such as detailed HI information. Analyses were conducted with SAS vers. 9.3, or SAS Enterprise, vers. 4.2[4] software (SAS Institute, Inc., Cary, NC).

For analyses, each stranding was considered a separate event, except for mass strandings and mother–calf pairs, where individual animals are not independent. For mother–calf pairs, maternity was either genetically determined or presumed on the basis of a combination of sex, age class, date, and proximity of an adult female to a calf. Mass strandings were defined as 2 or more individuals, excluding mother–calf pairs, of the same species at the same location (within 5 km from each other) on the same day. Two species were considered exceptions to this definition. Harbor porpoises (*Phocoena phocoena*) meeting these conditions were not considered a mass stranding because they do not travel in tight social groups (e.g., Raum-Suryan and Harvey, 1998) and, therefore, one animal beaching is unlikely to influence another animal beaching (Geraci and Lounsbury, 2005). Coastal bottlenose dolphins meeting the defined conditions also were not generally considered a mass stranding because of their high frequency of stranding and coastal abundance, except for one event where 3 animals stranded together alive.

For analyses of coastal bottlenose dolphins, stranding events were stratified by dolphin length and HI categories. There is a tendency for seasonal calving (Hohn, 1980; Thayer et al., 2003) and a concomitant high mortality of neonates (Fernandez and Hohn, 1998). The resulting preponderance of neonatal strandings can mask stranding patterns of older animals when all strandings are combined. Because documentation of neonatal characteristics (*see* Thayer et al., 2003) has not been consistent for all strandings, length was used as a proxy. In NC, Thayer et al. (2003) documented the maximum length of true neonates as 125 cm (mean=108.2 cm). Thus, all strandings <125 cm were categorized as perinates, although we recognize that this category could comprise most or all of the neonates, as well as some specimens up to 3 months of age (Fernandez and Hohn, 1998). Nonperinatal (≥125 cm) coastal bottlenose dolphin strandings were stratified into HI categories: HI-FI, HI-no, HI-CBD, and HI-other. For mother–calf pairs, the HI category of the mother was used. The sample size of the category HI-other was too small for analyses (n=26 events). Only 4 perinatal bottlenose dolphin strandings were positive for HI (HI-FI=2, HI-other=2); therefore, perinates were not stratified by HI category. Animals with an estimated or minimum length (such as that due to severed flukes) of <125 cm were excluded (91 individuals from 89 events).

Temporal patterns

Yearly and monthly patterns of stranding events were evaluated for taxonomic groups with sufficient sample sizes. When necessary to achieve adequate sample sizes, species with similar habitats were combined. Annual trends were assessed by using a simple linear regression (SAS PROC REG) for the following taxonomic groups: balaenopterids, pygmy sperm whales (*Kogia breviceps*); dwarf sperm whales (*Kogia sima*); harbor porpoises; harbor seals (*Phoca vitulina*); non-*Phoca* pinnipeds; non-*Kogia* pelagic odontocetes (delphinids except coastal bottlenose dolphins, ziphiids, and sperm whales [*Physeter macrocephalus*]), and the coastal bottlenose dolphin categories mentioned previously, including coastal and inshore strandings. For the simple regression only, data (plus 0.5 due to zeros) were natural log transformed. Monthly stranding patterns were

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

evaluated by using a maximum likelihood generalized linear model (GLM) (SAS PROC GENMOD) with a log link function and a Poisson error distribution, with month as the categorical predictor variable and number of strandings as the response variable (McFee et al., 2006). For each model, the month with the lowest mean count was used as the reference group. The model was evaluated for over-dispersion and goodness of fit by examining the magnitude of the deviance and the Pearson chi-square statistic divided by its degrees of freedom and by computing the probability of obtaining the observed chi-square statistic for each test. If over-dispersion or lack of fit occurred with either criterion, the model was rerun with a negative binomial error distribution and the fit was similarly evaluated. The lowest Akaike information criterion (AIC) values were used to determine the best fit. Harbor porpoise and harbor seal strandings were highly seasonal, causing nonconvergence in the GLM analysis. As a result, their seasonal patterns were described qualitatively. Sample sizes were too small to test for month effects for balaenopterids, dwarf sperm whales, and non-*Phoca* pinnipeds.

For species represented by a preponderance of small individuals, each stranded animal was assigned a maturity state on the basis of length relative to published length estimates: humpback whales (*Megaptera novaeangliae*) (Rice, 1963), common minke whales (*Balaenoptera acutorostrata*; hereafter 'minke whales') (Boyd et al., 1999), harbor porpoises (Read and Gaskin, 1990; Lockyer, 1995), harbor seals (Boulva and McLaren, 1979), hooded seals (*Cystophora cristata*) (Reeves et al., 1992), gray seals (*Halichoerus grypus*) (Bonner, 1981), and harp seals (*Pagophilus groenlandicus*) (Reeves et al., 1992; Hammill et al., 1995).

Spatial patterns

Spatial patterns were evaluated after stratifying the data into strandings recovered ocean-side or inshore. Relatively few strandings were recovered inshore; therefore, only qualitative results were presented. For the ocean-side analysis, the coast was stratified into 4 segments (A–D) with boundaries at the VA–NC line, each cape (Hatteras, Lookout, and Fear), and at the NC–SC line (Fig. 1). The coastline length of each segment was calculated in ArcGIS 10 software (Esri, Redlands, CA). Within each taxonomic group, a chi-square analysis was used to compare the number of observed strandings with an expected value proportional to the segment length. When a significant difference (P=0.05) was found, standardized residuals were examined to determine which coastal segments had significantly more or fewer strandings (i.e., standardized residuals $>|1.96|$). Delphinid species included in the taxonomic group of non-*Kogia* pelagic odontocetes were further divided into groupings that could be plotted in ArcGIS to qualitatively examine patterns not testable due to small sample sizes: 1) pilot whales, 2) pelagic delphinids generally associated with cool northern waters, 3) pelagic delphinids generally associated with warm southern waters, and 4) pelagic delphinids with a more cosmopolitan distribution in areas north and south of NC. Species whose distribution in the western North Atlantic are not well defined were assigned to one of the aforementioned categories on the basis of what is generally known of their distribution (e.g., melon-headed whales [*Peponocephala electra*] are generally a tropical–subtropical species; Perryman et al., 1994).

Because coastal bottlenose dolphin strandings were numerous enough to be investigated in more detail, the coastline was divided into 7 segments by dividing segments A–C in half (A1, A2, B1, B2, C1, C2) (Fig. 1). Segment D was not divided because it was already less than half the length of segments A–C. As with the 4-segment analyses, a chi-square analysis was used to determine whether the number of observed strandings per segment was significantly different from an expected value proportional to the segment length (P=0.05); standardized residuals were examined when a significant difference was found in order to identify which segments had significantly more or fewer strandings (i.e., standardized residuals $>|1.96|$).

To visualize the distribution of all strandings on a finer scale, the NC coast was divided into 10-km sections by using ArcGIS; the last (most southern) section was 7.6 km. Strandings were assigned to one of these 54 sections with ArcGIS. The mean annual strandings per section were graphed for coastal bottlenose dolphins and all other species combined.

Human interactions

Stranding data were stratified into the HI categories mentioned previously. The evidence for HI was reviewed for strandings categorized as HI-FI and HI-other. Unless FI lesions were noted as healed, they were assumed to be fresh. For HI-FI animals recovered with attached gear, totals were produced by gear type.

Results

During 1997 through 2008, 1847 individual marine mammal strandings were reported for 1777 events comprising 9 families and 34 species (Table 1). Species could not be determined for 67 strandings. The majority of individual strandings were coastal bottlenose dolphins (56%), harbor porpoises (13%), and harbor seals (4%) (Fig. 2). Nineteen of 185 bottlenose dolphins tested were confirmed genetically as being the offshore morphotype. *Kogia* spp. represented 5% of strandings; of those, pygmy sperm whales were found to be more common than dwarf sperm whales. There were 19 group stranding events, primarily those of *Kogia* spp. and coastal bottlenose dolphins, and mostly mother–calf pairs (Table 2). For 3 of the 9 mother–calf pairs of

Table 1

Annual totals of individual (inds.) marine mammal strandings (n=1847; 34 species) recovered from 1777 reported events (evts.) in North Carolina during 1997–2008.

Species by family	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	All inds.	All evts.
Balaenidae														
Eubalaena glacialis						1	1	1			1	1	5	5
Balaenopteridae														
Balaenoptera acutorostrata			2	1		2			2			1	8	8
Balaenoptera borealis								1					1	1
Balaenoptera edeni							1						1	1
Balaenoptera physalus		1					2						3	3
Megaptera novaeangliae	2	2		3	5	3	1	1		2	2	2	23	23
Unidentified balaenopterid	1	1										1	3	3
Delphinidae														
Delphinus delphis	2	2		6	16	4	8	4	1	2		1	46	40
Feresa attenuata		1										1	2	2
Globicephala macrorhynchus		1		1	1		1	1	37			3	45	13
Globicephala melas			2				2	1	1				6	6
Globicephala species							1		2	1		1	5	5
Grampus griseus	1	2	1		3	2	2	3	2	1		1	18	18
Lagenorhynchus acutus			1		1		1	2	4	1	1	3	14	14
Peponocephala electra										1		1	2	2
Pseudorca crassidens						1							1	1
Stenella attenuata						2	1						3	3
Stenella clymene			2	1				1					4	4
Stenella coeruleoalba	6	1		1	3	3	5	1	13	1	3	2	39	28
Stenella frontalis	1	2		3	2	2	3		2	1	2	1	19	18
Stenella longirostris	1				2								3	3
Stenella species	1	1											2	2
Steno bredanensis				1						2			3	3
Tursiops truncatus coastal	127	103	95	102	88	92	68	84	75	64	75	66	1039	1034
Tursiops truncatus offshore			1	1		2	3	6	3	2		1	19	19
Unidentified delphinid	1	2	1	2	4		2	1	3	2	1	4	23	23
Kogiidae														
Kogia breviceps	3	5	1	3	2	5	6	5	6	8	5	4	53	47
Kogia sima	1		6	4	1		2	2	4	7	7	1	35	27
Kogia species		1										1	2	2
Phocidae														
Cystophora cristata			1	1	5					4			11	11
Halichoerus grypus	1			1		1		2	2	2	2	1	12	12
Pagophilus groenlandicus	1		1			1	1	1	1	1			7	7
Phoca vitulina	1	11	2	8	4	3	15	4	12	5	2	6	73	73
Unidentified phocid				1					1	1		2	5	5
Phocoenidae														
Phocoena phocoena	25	4	59	6	21	5	38	15	43	6	20	7	249	249
Physeteridae														
Physeter macrocephalus		1	1	1		1	1	1		1		1	8	8
Trichechidae														
Trichechus manatus		2			1			1				1	5	5
Ziphiidae														
Mesoplodon densirostris					2			1	1	1	1	1	7	6
Mesoplodon europaeus		5	1		2	1	2		2				13	13
Mesoplodon mirus							1						1	1
Mesoplodon species		1									1		2	2
Ziphius cavirostris		1		1									2	2
Unidentified ziphiid		1			1								2	2
Unknown	3	1	2	1	1	2	3		4	1		5	23	23
Total	178	152	179	149	165	133	171	139	221	117	123	120	1847	1777

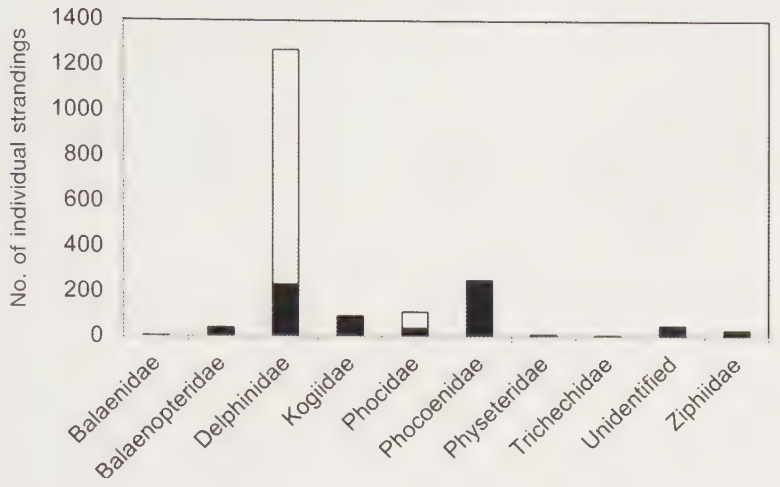

Figure 2

Number of marine mammal strandings (n=1847) reported in North Carolina during 1997–2008 by family. The families Delphinidae and Phocidae are subdivided to show the large contribution of a single species (white bars: coastal bottlenose dolphin [*Tursiops truncatus*] and harbor seal [*Phoca vitulina*] respectively) to other species in each family (black bars).

Kogia spp., the pair stranded with an adult male. Total length was measured (i.e., not estimated) for 570 females and 679 males identified to species (Table 3). The average length of the coastal bottlenose dolphins classified as perinates (n=179) was 105.8 cm (standard deviation [SD]=9.6). Of those dolphins, 28 were <95 cm, the size of the smallest measured neonate in NC during 1992–99 (Thayer et al., 2003).

Live strandings accounted for 15% of all strandings; more than 41% of pelagic odontocetes (40% of delphinids, 52% of *Kogia* spp., 15% of ziphiids, and 75% sperm whales) and 60% of pinnipeds were found alive. Of the 282 live strandings (233 cetaceans, 65 seals), 41% died on their own, 29% were euthanized, 15% were transferred to a rehabilitation facility (36 seals, 7 cetaceans), and 13% were immediately released or relocated. The fate was unknown for the remaining 2 animals, both dwarf sperm whales: 1) one animal was attacked by a shark at the time of the stranding, and 2) a calf was reported but gone when the

Table 2

Marine mammal stranding group events (mother–calf pairs, mass strandings) (n=19) during 1997–2008 in North Carolina.

Year	Month	Day	Species	Mother–calf pair	Mass stranding	No. of animals	Habitat
1997	Jan	6	*Tursiops truncatus* coastal	yes	no	2	Ocean
1998	Sep	13	*Kogia breviceps*	yes	no	2	Ocean
1999	Nov	11	*Kogia sima*	yes	no	2	Ocean
1999	Nov	29	*Kogia sima*	yes	no	2	Ocean
2000	Feb	9	*Stenella frontalis*	no	yes	2	Ocean
2000	Sep	15	*Kogia sima*	yes	no	2	Ocean
2001	Feb	1	*Delphinus delphis*	no	yes	7	Ocean
2001	Sep	21	*Mesoplodon densirostris*	yes	no	2	Ocean
2003	Apr	1	*Tursiops truncatus* coastal	yes	no	2	Ocean
2003	Nov	23	*Kogia breviceps*	yes	no	2	Ocean
2004	May	27	*Tursiops truncatus* coastal	yes	yes	3	Inshore
2005	Jan	15	*Globicephala macrorhynchus*	yes	yes	33	Ocean
2005	Jan	16*	*Kogia sima*	yes	yes	3	Ocean
2005	Aug	22	*Stenella coeruleoalba*	no	yes	12	Ocean
2006	Feb	17	*Kogia sima*	yes	yes	3	Ocean
2006	Sep	2	*Kogia breviceps*	no	yes	3	Ocean
2006	Oct	17	*Tursiops truncatus* coastal	yes	no	2	Ocean
2007	Feb	5	*Kogia sima*	yes	no	2	Ocean
2007	Jul	28	*Kogia breviceps*	yes	yes	3	Inshore

* Genetically confirmed calf recovered 19 January 2005.

Table 3

Measured lengths (cm) for marine mammal strandings identified to species and sex in North Carolina during 1997–2008. SD=standard deviation (SD). Min=minimum. Max=maximum.

	Female					Male				
Species by family	Mean	SD	Min	Max	*n*	Mean	SD	Min	Max	*n*
Balaenidae										
Eubalaena glacialis	1490.0				1	633.5	195.9	495	772	2
Balaenopteridae										
Balaenoptera acutorostrata	466.5	14.8	456	477	2	288.5	6.4	284	293	2
Balaenoptera borealis						1402.0				1
Balaenoptera edeni						1105.0				1
Balaenoptera physalus	1690.0				1	1720.0				1
Megaptera novaeangliae	831.7	76.5	745	890	3	889.1	91.0	763	1065	9
Delphinidae										
Delphinus delphis	201.1	8.2	182	211	17	210.8	24.2	121	229	20
Feresa attenuata						210.0	7.1	205	215	2
Globicephala macrorhynchus	336.0	48.4	210	387	26	309.5	122.3	156	506	12
Globicephala melas	350.0				1	342.0	181.0	214	470	2
Grampus griseus	240.6	30.7	187	261	5	242.8	50.2	164	321	10
Lagenorhynchus acutus	166.5	2.1	165	168	2	202.0	51.0	152	281	9
Peponocephala electra						247.0	1.4	246	248	2
Pseudorca crassidens	455.0				1					
Stenella attenuata	191.0				1					
Stenella clymene	189.0				1	174.3	35.0	135	202	3
Stenella coeruleoalba	195.8	26.4	156	217	5	214.2	27.0	152	241	30
Stenella frontalis	170.2	32.0	118	212	9	195.6	27.5	150	221	8
Stenella longirostris						230.0	2.8	228	232	2
Steno bredanensis	235.0				1	191.0				1
Tursiops truncatus coastal	199.3	58.7	85	285	334	196.5	59.3	88	334	377
Tursiops truncatus offshore	276.5	17.8	245	298	6	261.4	36.5	180	291	12
Kogiidae										
Kogia breviceps	241.1	59.1	117	312	16	276.1	43.7	154	346	31
Kogia sima	200.7	33.8	123	242	15	207.1	30.9	133	243	15
Phocidae										
Cystophora cristata	109.0	11.8	96	119	3	112.4	10.1	94	125	6
Halichoerus grypus	92.0	9.7	78	99	4	124.2	14.4	108	136	3
Pagophilus groenlandicus	114.0				1	103.0	17.0	91	115	2
Phoca vitulina	103.6	19.6	76	135	17	104.3	21.8	83	172	21
Phocoenidae										
Phocoena phocoena	117.9	13.6	84	169	80	115.4	9.0	99	154	79
Physeteridae										
Physeter macrocephalus	677.7	321.9	381	1020	3	872.3	407.5	416	1200	3
Trichechidae										
Trichechus manatus						298.5	9.9	288	310	4
Ziphiidae										
Mesoplodon densirostris	383.6	105.1	196	439	5	415.0	11.3	407	423	2
Mesoplodon europaeus	384.8	89.1	202	463	7	407.8	56.4	295	444	6
Mesoplodon mirus	478.0				1					
Ziphius cavirostris	484.5	55.9	445	524	2					

response team arrived. Attempted rehabilitation was chosen for a greater percentage of seals (55%) than for cetaceans (3%). The majority of seals (72%) and minority of cetaceans (2 of 7: 29%) were released after rehabilitation.

Temporal patterns

An average of 154 individual strandings (SD=30.6) or 148.1 stranding events (SD=23.8) were reported annually. The highest annual number of individu-

als was recorded in 2005 (n=221) and the lowest in 2006 (n=117) (Table 1). Annual totals of individual strandings were influenced by mass strandings and unusual mortality events (UMEs) (MMPA 16 USC 1361; Gulland, 2006). Two of the mass strandings occurred on consecutive days in January 2005 and were designated part of the same UME (Table 2) (Hohn et al., 2006). Also in 2005 was an UME of harbor porpoises (n=43) (Hohn et al., 2013) in the spring and a mass stranding of striped dolphins (n=12) in late summer. Although the number of strandings in 2004 was not high, there was an UME of pelagic small cetaceans (primarily pygmy sperm whales and offshore bottlenose dolphins) along the mid-Atlantic from July to September 2004 that included 13 strandings in NC.

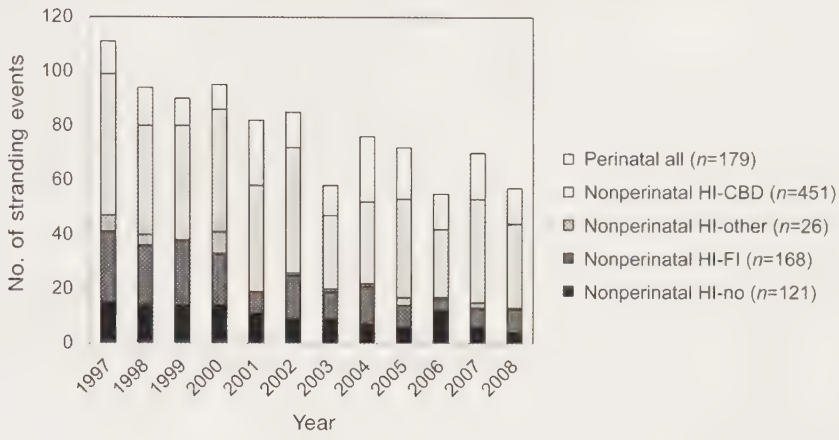

Figure 3

Number of annual stranding events for perinatal (<125 cm) and nonperinatal (≥125 cm) coastal bottlenose dolphins (*Tursiops truncatus*) in North Carolina. Nonperinatal strandings are divided into human interaction (HI) categories: HI-CBD (could not be determined), HI-other (e.g., mutilation, vessel strike), HI-FI (fishery interaction), and HI-no (no evidence of HI).

Annual trends were detected only for coastal bottlenose dolphins. The average annual number of coastal bottlenose dolphin strandings was 86.6 (SD=18.6) (Table 1), of which the average for perinates was 14.3 (SD=5.2; range: 9 [1999 and 2000] to 24 [2001 and 2004]). A significant negative annual trend was detected for all tested categories of nonperinatal bottlenose dolphin stranding events (HI-FI, n=168, P<0.001; HI-no, n=121, P=0.002; HI-CBD, n=451, P=0.05). No trend was detected for perinates (n=179, P=0.75) (Fig. 3) or for the second and third most numerous species, harbor porpoises (n=249, P=0.59) and harbor seals (n=73, P=0.86), both of which fluctuated greatly among years (Table 1). In addition, no annual trend was detected for balaenopterids, pygmy sperm whales, dwarf sperm whales, non-*Kogia* pelagic odontocetes, or non-*Phoca* pinnipeds. Strandings of baleen whales occurred at low levels, but there were never fewer than 2 per year. All 5 right whales stranded during or after 2002.

Significant month effects (GLM, all P<0.0001) were found for non-*Kogia* pelagic odontocetes and all tested categories of coastal bottlenose dolphin events except HI-no (P=0.69), and no month effect for the other groups or species. For many species, strandings peaked in the spring (Table 4, Fig. 4). HI-FI and HI-CBD bottlenose dolphins had a second peak in the fall.

Other species or species groups showed general seasonal patterns (Table 4). Although there were relatively few sperm whale strandings (n=8), all occurred between December and June. Baleen whales also were notably absent during summer months (June–August) (Fig. 4). Minke whales and humpback whales were all immature according to their length (Table 3). Of the 8 minke whale strandings, 2 were likely newly weaned and 2 were dependent calves. Harbor porpoises occurred exclusively from January through May, with 78% of the strandings during March and April (Fig. 4). Of the 184 measured harbor porpoises, 96% (n=177) were immature on the basis of length and 70% (n=128) were approximately 1 year old or less. Harbor seals occurred in every month, except August, although 86% stranded between January and April (Fig. 4). Eleven of 12 gray seals stranded from February through May (Table 4). In contrast, 73% of hooded seals stranded during July–September. Hooded and gray seals were all immature on the basis of length, whereas 85% of harbor seals and 86% of harp seals were immature.

Spatial patterns

Strandings were not uniformly distributed. Of the 1847 strandings documented, 88% (n=1624) occurred ocean-side and included 1557 events (0.24 events per km of ocean coastline). Of the ocean-side stranding events, 46% occurred north of Cape Hatteras (160 km or 30% of coast), and 76% occurred north of Cape Lookout (>280 km or 52% of coast) (Figs. 5 and 6). For all tested categories of coastal bottlenose dolphins except HI-no (χ^2=3.9, n=101, P=0.69), there was a segment effect (7 ocean-side segments, A1–D) (perinatal, χ^2=26.2, n=161, P=0.0002; nonperinatal HI-FI, χ^2=26.8, n=145, P=0.0002; nonperinatal HI-CBD, χ^2=62.9, n=357, P<0.0001) (Fig. 7). On the basis of standardized residuals (>|1.96|), segment B1 had significantly more strandings than expected for these 3 significant categories. For all other significant segments, observed strandings were less than expected

Table 4

Monthly totals of individual (inds.) marine mammal strandings (n=1847) recovered from 1777 reported events (evts.) in North Carolina during 1997–2008.

Species by family	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	All inds.	All evts.
Balaenidae														
Eubalaena glacialis			1	1					1		1	1	5	5
Balaenopteridae														
Balaenoptera acutorostrata	1	1	1	2	1					1	1		8	8
Balaenoptera borealis		1											1	1
Balaenoptera edeni			1										1	1
Balaenoptera physalus		1	1		1								3	3
Megaptera novaeangliae	1	2	4	4					1		2	9	23	23
Unknown balaenopterid	1	1	1										3	3
Delphinidae														
Delphinus delphis	1	12	11	9	6				1		1	5	46	40
Feresa attenuata					1			1					2	2
Globicephala macrorhynchus	33	3	1	1	1		2		2	1		1	45	13
Globicephala melas		1	1	1	2						1		6	6
Globicephala species				3	1					1			5	5
Grampus griseus	1		1	3	2	3		2	2	2	2		18	18
Lagenorhynchus acutus		1	5	8									14	14
Peponocephala electra					1		1						2	2
Pseudorca crassidens					1								1	1
Stenella attenuata			1	2									3	3
Stenella clymene		1			1			1			1		4	4
Stenella coeruleoalba	2	6	1	6	2	1		14	1	1	2	3	39	28
Stenella frontalis		4	3	1	2	1	1	3	1	1		2	19	18
Stenella longirostris			3										3	3
Stenella species								1		1			2	2
Steno bredanensis	2							1					3	3
Tursiops truncatus coastal	73	78	105	200	172	61	33	49	31	92	94	51	1039	1034
Tursiops truncatus offshore		2	2	1		1	6	5		1	1		19	19
Unidentified delphinid	2	1	3	5	5	2			2	2		1	23	23
Kogiidae														
Kogia breviceps	3	4	3	10	1	4	6	4	9	2	6	1	53	47
Kogia sima	7	9	1	2	3	1	2	1	2		5	2	35	27
Kogia species		1			1								2	2
Phocidae														
Cystophora cristata			2		1		2	4	2				11	11
Halichoerus grypus		2	4	3	2			1					12	12
Pagophilus groenlandicus	2	2		2					1				7	7
Phoca vitulina	12	18	25	8	1	1	1		2	1	2	2	73	73
Unidentified phocid			1	3	1								5	5
Phocoenidae														
Phocoena phocoena	2	39	139	55	14								249	249
Physeteridae														
Physeter macrocephalus	1		2	2		2						1	8	8
Trichechidae														
Trichechus manatus	1						1	1				2	5	5
Ziphiidae														
Mesoplodon densirostris	1		1			1			3		1		7	6
Mesoplodon europaeus	1		1	1	1	3	1	4	1				13	13
Mesoplodon mirus										1			1	1
Mesoplodon species				1								1	2	2
Ziphius cavirostris					1	1							2	2
Unidentified ziphiid					1	1							2	2
Unknown	1	1	2	3	3	3	2	0	3	3	1	1	23	23
Total	148	191	327	337	229	86	58	92	65	110	121	83	1847	1777

(segments C2 and D for HI-CBD, segments B2 and C2 for HI-FI, and segment C2 for perinatal strandings).

There was a significant difference in number of ocean-side stranding events among the 4 segments (A–D) for harbor porpoises (χ^2=176.1; P<0.0001, n=247), non-*Kogia* pelagic odontocetes (χ^2=55.1; n=206, P<0.0001), harbor seals (χ^2=17.8; n=67, P=0.0005), and non-*Phoca* pinnipeds (χ^2=11.4; n=34, P<0.0096) (Fig. 7), and no segment effect for the other groups or species. Segment A had significantly more events than expected and segment C less than expected for all 4 taxonomic groups. In addition there were significantly fewer than expected harbor porpoises, harbor seals, and non-*Kogia* pelagic odontocetes in segment D and fewer than expected harbor porpoises in segment B. The spatial patterns of non-*Kogia* pelagic odontocetes were driven by the pelagic delphinids, which represented the majority of this taxonomic group. Generally, all 4 subcategories of pelagic delphinids, including southern species, stranded primarily north of Cape Hatteras (Fig. 6). For pilot whales, the more southerly short-finned pilot whale occurred in all 4 segments, whereas the more northerly long-finned species (*Globicephalus melas*) was never recovered south of Cape Hatteras. More northern pelagic delphinid individuals (n=99) were recovered than southern delphinid individuals (n=17); no stranding within either group was recovered in segment D (Fig. 6). Cosmopolitan pelagic delphinids (n=57) were recovered in all segments. Although samples sizes of the individual species did not allow for statistical analysis, the overall spatial distribution of strandings demonstrated the preponderance of strandings in coastal segment A and a clustering of strandings just south of Cape Hatteras and Cape Lookout. Harbor seals and other seals showed the same patterns of differences among segments; however, a map of sightings shows that although harbor seals were recovered from the VA line to southwest of Cape Fear (segment D), the other seals were never recovered very far south of Cape Lookout.

The spatial pattern of balaenopterids was pronounced despite no statistical difference (P=0.39) among the 4 coastal segments. Of the 36 ocean-side strandings, 42% occurred north of Cape Hatteras (segment A) and 69% occurred north of Cape Lookout (segments A and B). Seven of the 10 whales within segment C were recovered in the northern 30 km (Fig. 6). Interestingly, 3 of the 8 minke whales stranded in segment C, just inside the bight at Cape Lookout, and another minke whale stranded inshore of the bight about 10 km into the sound.

The majority (83%) of inshore strandings were those of coastal bottlenose dolphins (183 of 223). All manatees (n=5) were recovered inshore. There were 2 harbor porpoises recovered far inshore, both in 2005 and both found alive. Some nonestuarine species (e.g., humpback whale, sperm whale, offshore bottlenose dolphin) were also recovered inshore, but generally near inlets (Fig. 6).

Human interactions

Most strandings (60%; n=1096) were HI-CBD (Table 5). Human interactions (HI) were reported for 299 (16%) strandings, including 18 of the 34 species examined, as well as 5 carcasses unidentified to species (Table 5). The HI-yes category represented about 40% of those for which it was possible to determine whether an interaction occurred (excludes HI-CBD). Overall, most (80%) of the HI-yes strandings were HI-FI. For 5 species, there were 10 or more HI strandings: coastal bottlenose dolphins, harbor porpoises, short-finned pilot whales, harbor seals, and humpback whales. The percentage of HI was particularly high for humpback whales and coastal bottlenose dolphins (Table 5). The incidence of HI-FI of those for which it was possible to determine whether an interaction occurred was similar for coastal bottlenose dolphins recovered inshore (28 out of 60; 47%) and ocean-side (153 out of 331; 46%). Healed FI lesions were noted on 20 strandings: pilot whales (n=10), a common dolphin (n=1), striped dolphins (n=2), a coastal bottlenose dolphin (n=1), a Risso's dolphin (n=1), and humpback whales (n=5). All of the pilot whales with healed lesions were part of the 2005 mass stranding, and had no other evidence of HI. The Risso's dolphin also had fresh FI lesions. Of the humpback whales with healed FI lesions, one was caught in a gill net and died and one stranded dead with trauma consistent with a vessel strike. Two harbor porpoises and 24 coastal bottlenose dolphins classified as HI-FI were also mutilated; they had missing appendages or cuts into the abdomen, or both. Harbor porpoise strandings classified as HI-FI occurred in February (n=3), March (n=3) and April (n=5).

Of the 44 animals entangled in fishing gear (active or free-floating gear) or with ingested fishing gear, gill net, hook-and-line, and trap or pot line gears were the most prevalent (Table 6). Seven animals were released alive. In addition to these strandings, the network documented a humpback whale in February 2001 with a gill net caught on barnacles on its flukes. It was not considered stranded because it freed itself.

Evidence for HI-other (n=62) took several forms with mutilation being the most common (60%) (Table 5). In 3 cases, mutilation was known to have occurred after the stranding had been reported. Most of the mutilated coastal bottlenose dolphins, except for the one mutilated after it had stranded, and all of the harbor porpoises were CBD for FI. The mutilation for 20 of the 25 the dolphins and 7 of the 8 harbor porpoises was similar to that seen in HI-FI strandings with mutilation: clean cuts where fins or flukes were removed, ventral body slits, or both. The debris (e.g., "parachute cord" and thick rope) found entangled on 2 coastal bottlenose dolphins could not be confirmed as fishery-related. Harassment was recorded for 2 cetaceans: a pygmy sperm whale that was pushed back into the water 10 times before stranding responders

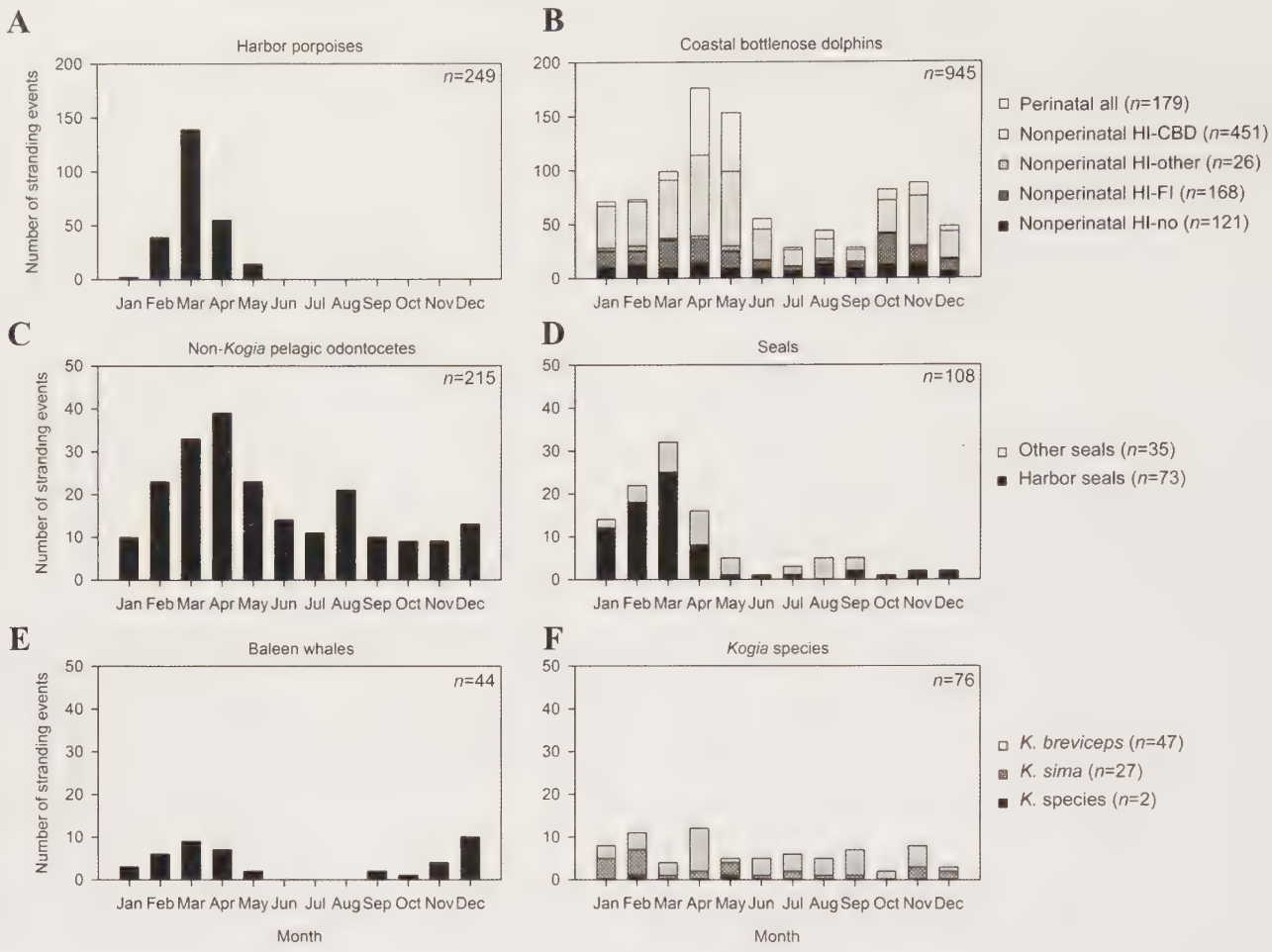

Figure 4

Monthly stranding events in North Carolina during 1997–2008 for (**A**) harbor porpoises (*Phocoena phocoena*), (**B**) perinatal (<125 cm) and nonperinatal (≥125 cm) coastal bottlenose dolphins (*Tursiops truncatus)*, (**C**) non-*Kogia* pelagic odontocetes, (**D**) seals, (**E**) baleen whales, and (**F**) *Kogia* species. Nonperinatal bottlenose dolphins strandings are divided into human interaction (HI) categories: HI-CBD (could not be determined), HI-other (e.g., mutilation, vessel strike), HI-FI (fishery interaction), and HI-no (no evidence of HI). Seals are divided into harbor seals (*Phoca vitulina*) and other seals. *Kogia* species are divided into pygmy sperm whales (*K. breviceps*), dwarf sperm whales (*K. sima*), and *Kogia* whose species were not identified. Note that *y*-axes in the top graphs are at a different scale than that of the other graphs.

arrived and a Risso's dolphin that the public tried to move when they heard it was going to be euthanized. Although cetaceans pushed off the beach were not generally classified as HI-other, these 2 animals were classified as HI-other because of excessive harassment. Harassment was more common for seals and included instances of the public trying to move or pick up the animal (n=4), resulting in one person being bitten, and instances where relocation was necessary because of persistent disturbance (n=2). Most of these seals were healthy, exhibiting normal haul-out behavior, and would not otherwise have met the definition of stranded.

Discussion

Biodiversity

A diverse array of marine mammal species strand in NC, reflecting the rich biodiversity of cetacean and pinniped fauna in nearby waters. Along a coastline of 537 km (<3 degrees of latitude), strandings included 9 families and 34 species (29 cetaceans; 4 pinnipeds; 1 manatee), ranging from tropical delphinids to pagophilic (ice-obligate) seals. This diversity is higher than that of other areas such as northwest Spain (15 marine mammal species along 1195 km, López et al., 2002), Hawaii

(16 odontocete species; Maldini et al., 2005), San Diego, California (24 cetacean species along 125 km, Danil et al., 2010), southeastern Canada (19 cetacean species, Nemiroff et al., 2010), and Cape Cod-southeastern Massachusetts (16 marine mammal species along 1126 km, Bogomolni et al., 2010). An exception is Western Australia where 34 cetacean species were found, but the study encompassed 12,889 km of coastline and roughly 20 degrees of latitude (Groom and Coughran, 2012). The high diversity found in NC emanates from multiple oceanographic features and the resulting 2 converging biogeographic zones off the coast. These findings may also reflect shifting distribution patterns over time that are indicative of climate change (e.g., MacLeod et al., 2005, Johnston et al., 2012).

A comparison of strandings to published records of live animals indicates that generally the most numerous stranded species inhabit nearshore waters, are very abundant, or both. Coastal bottlenose dolphins are the most abundant species nearshore, although their abundance varies seasonally (~1000–13,000 animals; Waring et al., 2010). Harbor porpoises and harbor seals generally inhabit coastal waters during at least part of the year (Bigg, 1981; Palka et al., 1996), although they are only seasonally present off NC and their local abundances and distribution are unknown. Relative stranding frequencies of pelagic delphinids generally reflect relative abundance during aerial and shipboard surveys (Waring et al., 2007). This is particularly interesting for species for which NC is their southern distribution (e.g., common dolphins, striped dolphins, Atlantic white-sided dolphins) (Waring et al., 2007). During summer surveys outside of the 10-m isobath along the mid-Atlantic coast of the United States, the most commonly sighted species were offshore bottlenose dolphins, sperm whales, Atlantic spotted dolphins and Risso's dolphins (Mullin and Fulling, 2003), and all of these species, except sperm whales, were quite often found stranded. In contrast, the prevalence of *Kogia* strandings is disproportionate to their relatively low population size estimate (pygmy sperm whales, n=741; dwarf sperm whales, n=1042) and pelagic distribution (Waring et al., 2013). This incongruity between stranding levels and population sizes for kogiids has been reported elsewhere (Maldini et al., 2005), and is likely due, in part, to population estimates that are underestimated owing to availability and perception bias during surveys (Barlow, 1999). Gervais' beaked whales (*Mesoplodon europaeus*) were also commonly stranded in this study, consistent with previous reports of this species stranding along the U.S. Atlantic coast (Waring et al., 2009a). As with *Kogia* species, the number of strandings is disproportionate to the low abundance estimate (*Mesoplodon* spp. and *Ziphius* spp. combined; n=3513; CV=0.63) (Waring et al., 2009a), and the species are also subject to the same detection biases during surveys. Some species (e.g., melon-headed whales, pygmy killer whales, false killer whales) that are rarely seen in the western North Atlantic (Mullin and Fulling, 2003; Waring et al., 2007) were also uncommon in the stranding record.

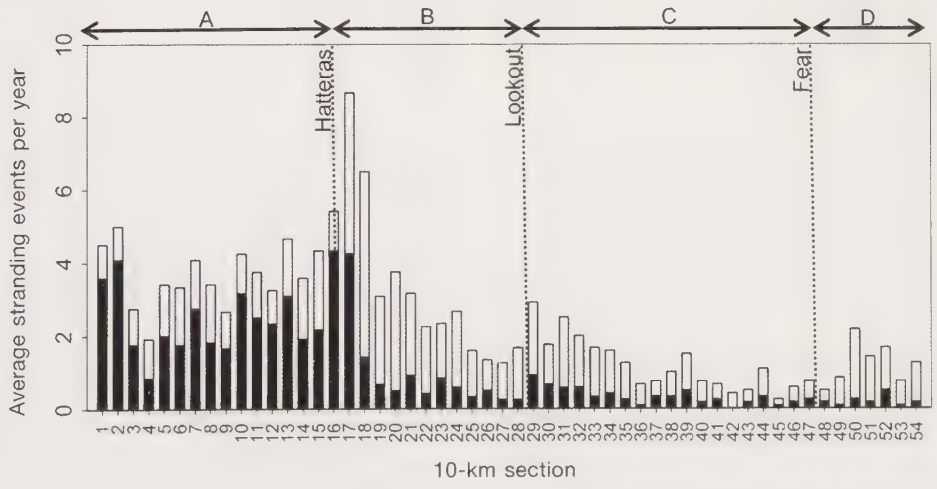

Figure 5

Mean annual stranding events by 10-km section within coastal segments (A–D) from the Virginia/North Carolina (NC) border (section 1) to the NC/South Carolina border (section 54; section=7.6 km) during 1997–2008. Graph shows coastal bottlenose dolphin (*Tursiops truncatus*) (white bars; n=855) separate from all other species (black bars; n=702). Vertical dotted lines indicate the areas of the 3 NC capes (Hatteras, Lookout, Fear) and divide the coastline into 4 segments: A, B, C, D.

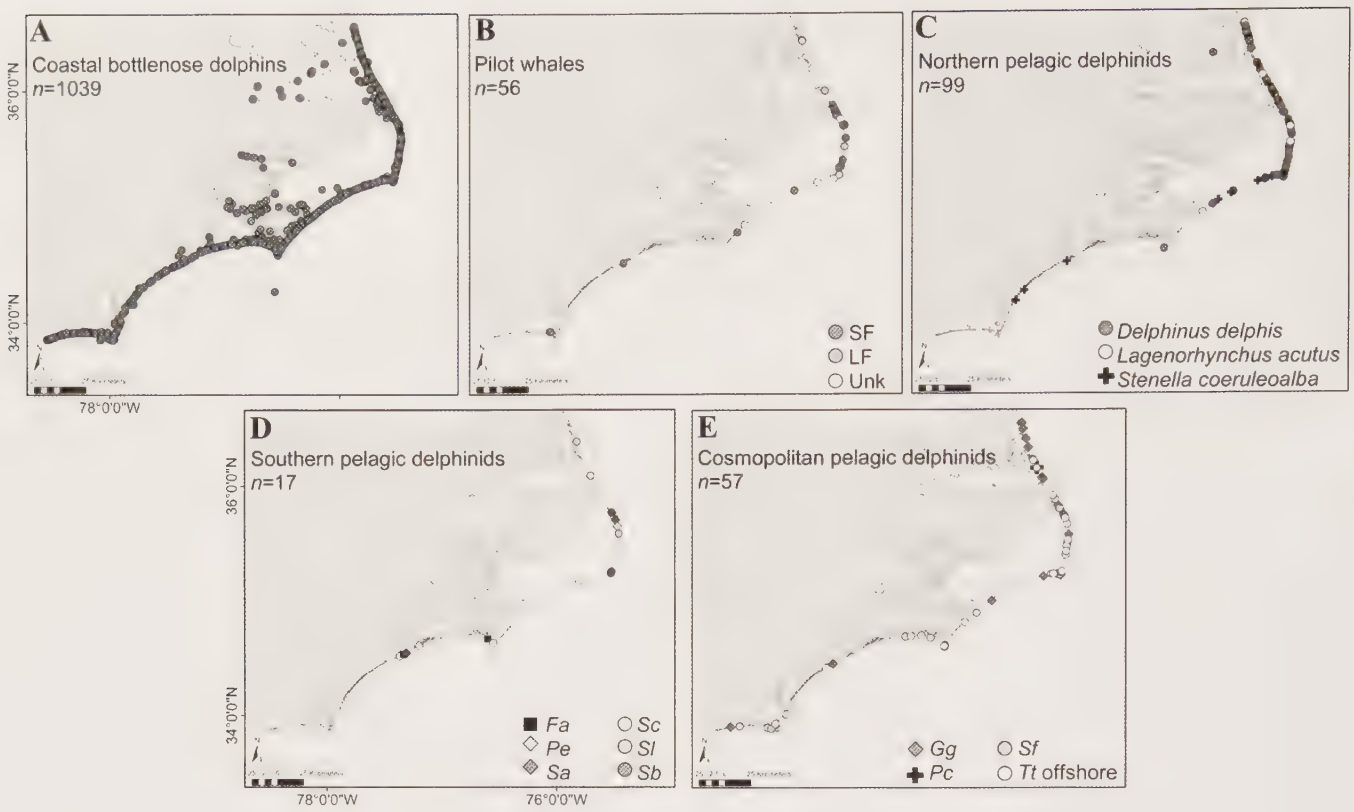

Figure 6

Locations of strandings in North Carolina during 1997–2008 by species or taxonomic group. (**A**) The ocean coastline is divided into 7 segments for coastal bottlenose dolphins (*Tursiops truncatus*) (from north to south: A1, A2, B1, B2, C1, C2, D) and (**B–K**) the ocean coastline is divided into 4 segments for all other taxonomic groups (from north to south: A, B, C, D). Map B: SF=short-finned pilot whales (*Globicephala macrorhynchus*), LF=long-finned pilot whales (*G. melas*), and Unk=unknown. Map D: southern pelagic delphinids—*Fa* (*Feresa attenuata*), *Pe* (*Peponocephala electra*), *Sa* (*Stenella attenuata*), *Sc* (*Stenella clymene*), *Sl* (*Stenella longirostris*), and *Sb* (*Steno bredanensis*). Map E: cosmopolitan pelagic delphinids—*Gg* (*Grampus griseus*), *Pc* (*Pseudorca crassidens*), *Sf* (*Stenella frontalis*), and *Tt* (*Tursiops truncatus*) offshore.

Spatiotemporal patterns

Seals In the western North Atlantic, seals generally occur at higher latitudes than those of NC. New Jersey is considered the prevalent southern distribution for harbor seals (Burns, 2009) and southeastern Canada for hooded and harp seals (McAlpine and Walker, 1990, McAlpine et al., 1999). Extralimital records exist from sightings but strandings are also an indicator of such extralimital movements. For example, juvenile harp seals have been reported as far south as Cape Henry, Virginia, (McAlpine and Walker, 1990), as well as having been stranded in NC. In contrast, although gray seals breed as far south as Massachusetts, their reported occurrence south of New Jersey is known only from strandings (Waring et al., 2013). Although the occurrence of extralimital records of hooded and harp seals has increased since the early 1990s (McAlpine and Walker, 1990; McAlpine et al., 1999), neither species was abundant in the current data set, despite stranding in most years. Extralimital sightings of hooded seals may be more common than those of harp seals overall; they are certainly more wide ranging, with reports as far south as Puerto Rico and the U.S. Virgin Islands (Mignucci-Giannoni and Odell, 2001). Nonetheless, in NC, harbor seals were recovered much farther south than hooded seals.

Although seal strandings occurred in every month and in all coastal segments, their occurrence primarily in winter and north of Cape Hatteras is consistent with general patterns of seal migration. Hooded seals were an exception with most strandings in the summer, including the southernmost records (McAlpine et al., 1999; Mignucci-Giannoni and Odell, 2001). In addition, the strandings of predominantly immature seals in NC may be indicative of age-segregated migration in which juveniles may be more likely to travel this far south or may be more likely to stay closer to shore than adults during winter, or may be indicative of greater mortality of immature animals while off NC.

For seals, human interactions were predominately a result of bycatch or harassment of live seals on the beach. The presence of these seals on the beach elicited great public interest because they are infrequent

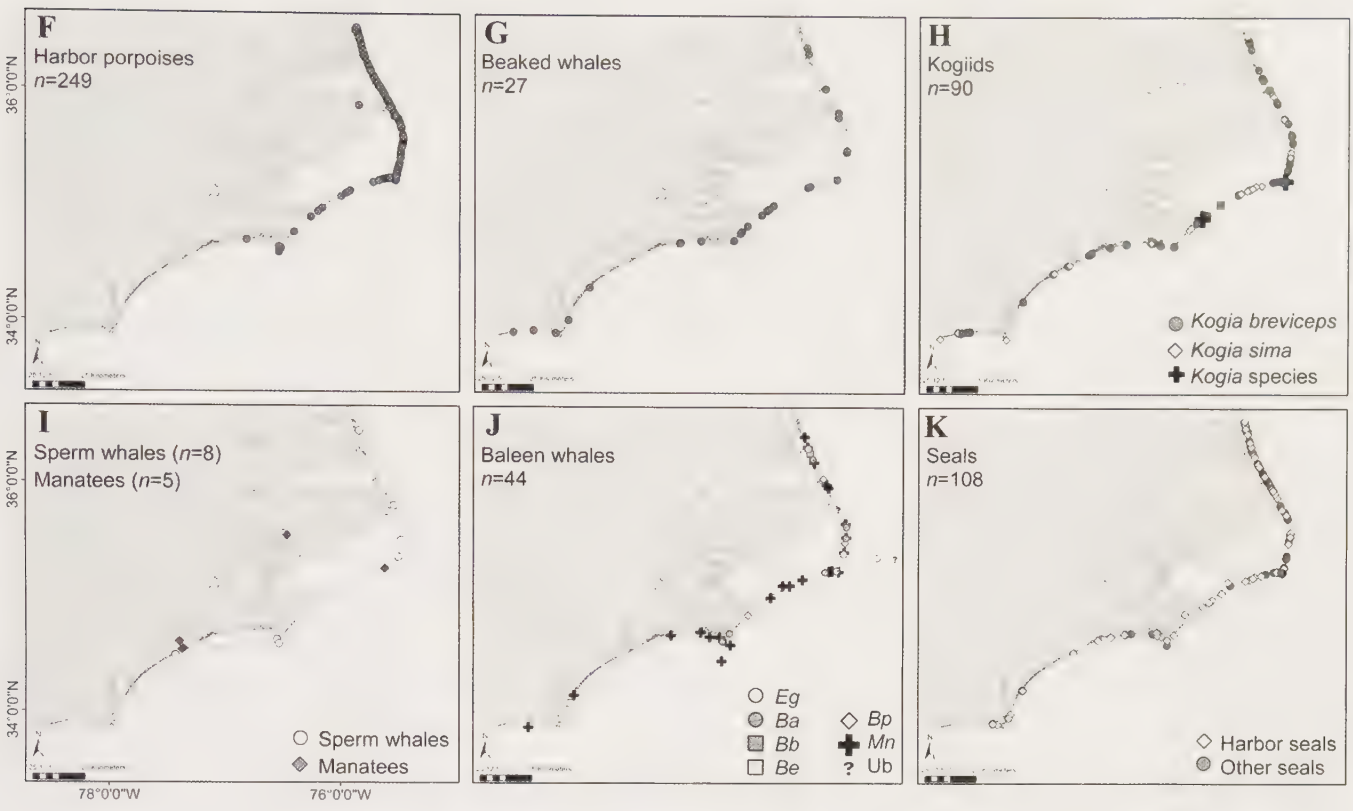

Figure 6 (*continued*)

Map J: baleen whales—*Eg* (*Eubalaena glacialis*), *Ba* (*Balaenoptera acutorostrata*), *Bb* (*Balaenoptera borealis*), *Be* (*Balaenoptera edeni*), *Bp* (*Balaenoptera physalus*), *Mn* (*Megaptera novaeangliae*), and Ub (Unknown balaenopterid). The baleen whales far from shore were found floating and towed to shore for necropsy when possible.

visitors and, at times, it was a challenge to maintain the safety of both seals and humans. The NC stranding network has increased outreach efforts to educate the public on the needs and dangers of hauled-out seals and on the legal mandates to protect seals from harassment (MMPA, 16 USC 1361).

Anecdotal evidence suggests that there has been an increase in the number of seals overall on NC and VA beaches (S. Barco, personal observ.). No trend was detected through the years of data included in this study, although there was interannual variability with notably high strandings in 2003 and 2005. Although the populations of some species are increasing (Waring et al., 2013), the drivers affecting an associated expansion of movements may not result in regular and increased movements to NC. Strandings, however, do not reflect the number of seals on the beach because they do not include healthy seals unless they were harassed. In addition, a standardized mechanism for reporting and tracking sightings, which is needed to test any hypothesized increase, has been lacking.

Harbor porpoise Interannual variability was the prevalent annual pattern for harbor porpoise strandings. Although harbor porpoises are known to be caught in gill nets (Orphanides, 2009), the number of HI-FI strandings was not high enough to explain increased strandings during some years (Hohn et al., 2013). Because harbor seals and porpoises occur in NC during a similar time of year and originate from northern waters, their marked increases during the same years may be a result of the same processes.

The temporal occurrence of harbor porpoise strandings in NC is consistent with the migration of porpoises out of northern areas as water temperatures decrease (Gaskin, 1992). The wintering grounds and migration patterns of harbor porpoises migrating south to the mid-Atlantic are poorly understood, but there is evidence that some porpoises may occur in offshore waters (*see* Palka et al., 1996). Although Cape Hatteras has been the presumed southerly limit (*see* Palka et al., 1996), 13% of strandings occurred between Cape Hatteras and Cape Lookout, owing either to drifting carcasses or to porpoises swimming south of Cape Hatteras at least occasionally. Interestingly, as with strandings of harbor seals, most harbor porpoise strandings were of sexually immature individuals (*see* also Hohn et al., 2013), the drivers for which may also be age-segregated migration and age-specific mortality patterns.

Harbor porpoises migrating along the western North Atlantic coast are susceptible to entanglement in fishing gear. Indeed in NC stranded harbor porpoises were

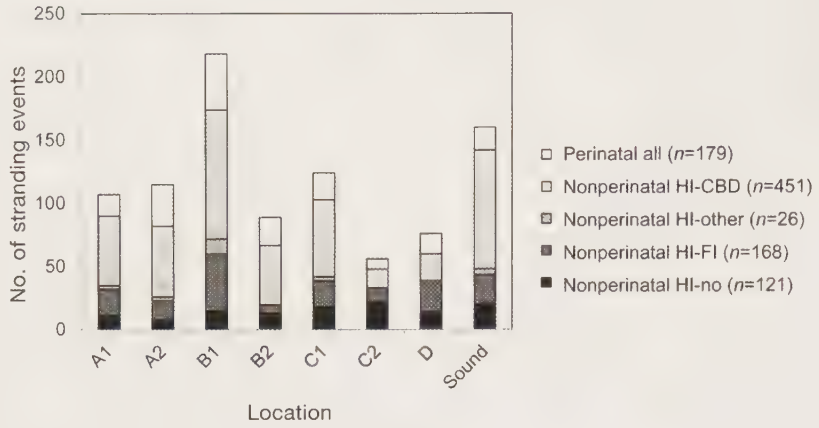

Figure 7

Spatial distribution of perinatal (<125 cm) and nonperinatal (≥125 cm) coastal bottlenose dolphins (*Tursiops truncatus*) stranding events by coastal segments (A1–D) and inshore in North Carolina during 1997–2008. Nonperinatal strandings are divided into human interaction (HI) categories: HI-CBD (could not be determined), HI-other (e.g., mutilation, vessel strike), HI-FI (fishery interaction), and HI-no (no evidence of HI).

found with fresh entanglement lesions that indicated that the entanglement occurred nearby. In addition, mutilation in the form of missing appendages, slit abdomens (or both) was noted on harbor porpoises that were HI-FI and on carcasses that were HI-other but CBD for FI. These types of mutilations are thought to be a result of fishermen's attempts to remove bycaught animals from gear, or to increase the possibility that the carcass would sink and not be recovered (or both) (Kuiken et al., 1994; Read and Murray, 2000). Most bycatch has been documented from New Jersey and north (Orphanides, 2009). However, data for the latest bycatch estimate were collected in February and March (Orphanides[5]), whereas more harbor porpoise strandings in NC were recovered in April than in February and many of those strandings were positive for FI. Observed trips and associated data used to calculate bycatch estimates of harbor porpoises off NC should therefore be expanded to April to ensure representative coverage of fisheries during months when harbor porpoises are present.

Pelagic odontocetes The distribution of pelagic odontocete strandings is likely influenced by the narrow shelf and proximity of the Gulf Stream to the coast (Cione et al., 1993) because habitat for many of these species is near the shelf break and at Gulf Stream fronts (Kenney and Winn, 1986; Hamazaki, 2002). Even southern species occurred north of Cape Hatteras; those species with oceanic distributions likely are associated with the Gulf Stream, as it approaches Cape Hatteras and remains close to shore north of the Cape before it meanders east, or with warm-water eddies (Gray and Cerame-Vivas, 1963) that can move shoreward.

Although pelagic odontocetes are a diverse group, across species they were often found alive or with evidence of having stranded alive, such as sand in the blowhole and abrasions or bruising on the ventrum and ventral flukes. Most live cetaceans died on their own before or shortly after stranding responders arrived. Animals recovered freshly dead (Geraci and Lounsbury, 2005) likely traveled nearshore and died shortly before or after stranding, but before the animal was discovered (Mead[3]). Individuals that died in their normal habitat far from shore would be less likely to be pushed by wind and currents and be deposited on the beach (Peltier et al., 2012). In some cases, the public pushed live animals back into the water—an action rarely chosen by stranding responders. The fates of animals pushed back are unknown except for a few instances where presumably the same animal restranded nearby. Decisions on the best course of action for other live strandings were made after responders consulted with veterinarians and the regional stranding coordinator. Euthanasia was chosen as the most humane treatment for most cetaceans (see Moore et al., 2007), in contrast to rehabilitation being a more suitable option for most seals.

Non-*Kogia* pelagic odontocetes generally stranded from February to May north of the zoogeographical and oceanographic boundary at Cape Hatteras. This trend was driven by species with the most stranding events: common dolphins and striped dolphins. Common dolphins and striped dolphins are generally northern species and occur most commonly off NC in winter (CeTAP[6]); this spatiotemporal distribution is similar to that found for harbor seals and harbor porpoises. Southern pelagic delphinids were less common, and despite their primarily southern distribution, generally showed the same spatiotem-

[5] Orphanides, C. D. 2011. Estimates of cetacean and pinniped bycatch in the 2009 northeast sink gillnet and mid-Atlantic gillnet fisheries. U.S. Dep. Commer. Northeast Fish. Sci. Cent. Ref. Doc. 11-08, 28 p. [Available from Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1026 or http://docs.lib.noaa.gov/noaa_documents/NMFS/NEFSC/NEFSC_reference_documnet/NEFSC_RD_11_08.pdf , accessed January 2013.]

[6] CeTAP (Cetacean and Turtle Assessment Program). 1982. A characterization of marine mammals and turtles in the mid- and north Atlantic areas of the U.S. outer continental shelf. Final Report, Contract AA51-C78-48, 538 p. Bureau of Land Management, Washington, D.C.

Table 5

Categories of human interaction (HI) for marine mammal strandings in North Carolina during 1997–2008: HI-FI (fishery interaction), HI-other (other HI evidence), HI-no (no evidence of HI), and HI-CBD (could not be determined). HI-other types are: mutil. (mutilation), vessel strike, ingest. plastic (ingested plastics), entangl. debris (entanglement in debris), gunshot (gunshot injury), and harass. (harassment). Each species or other taxonomic category with at least one record positive for (HI) is listed separately from "Other species".

		HI-other								
Species by family	HI -FI	Mutil.	Vessel strike	Ingest. plastic	Entangl. debris	Gun shot	Harass.	HI-no	HI-CBD	Total
Balaenidae										
Eubalaena glacialis	1		1					1	2	5
Balaenopteridae										
Balaenoptera acutorostrata	2							1	5	8
Balaenoptera edeni	1									1
Balaenoptera physalus			1						2	3
Megaptera novaeangliae	10		1					1	11	23
Unidentified balaenopterid	1								2	3
Delphinidae										
Delphinus delphis	2							22	22	46
Globicephala macrorhynchus	11	2		1				14	17	45
Grampus griseus	1						1	9	7	18
Stenella coeruleoalba	2							29	8	39
Tursiops truncatus coastal	181	25	3	1	2			179	648	1039
Tursiops truncatus offshore	2							15	2	19
Unidentified delphinid	2								21	23
Kogiidae										
Kogia breviceps							1	32	20	53
Phocidae										
Cystophora cristata							1	6	4	11
Halichoerus grypus							1	5	6	12
Phoca vitulina	9		1			2	4	24	33	73
Phocoenidae										
Phocoena phocoena	11	8						33	197	249
Physeteridae										
Physeter macrocephalus				1				3	4	8
Ziphiidae										
Mesoplodon densirostris				1				3	3	7
Mesoplodon europaeus				2				7	4	13
Other										
Unknown marine mammal	1	2							20	23
Other species								68	58	126
Total	237	37	7	6	2	2	8	452	1096	1847

poral stranding pattern as that of northern species. Those species with a more cosmopolitan distribution also were found most often north or just south of Cape Hatteras, but in contrast to the more northern or southern species, they, along with beaked whales, also stranded southwest of Cape Fear. Strandings of beaked whales were too few to detect trends, although the 2 months with the greatest number of Gervais' beaked whales were during summer.

Spatially, strandings of *Kogia* were similar to those of the cosmopolitan non-*Kogia* pelagic odontocetes. Although dwarf sperm whales have more tropical distribution than pygmy sperm whales (Chivers et al., 2005), the 2 species showed no obvious difference in their stranding distribution. Temporally, in contrast to the non-*Kogia* pelagic odontocetes, neither *Kogia* species showed a significant monthly pattern, which may be due to small sample sizes or presence offshore throughout the year.

The majority of fishery interactions among pelagic odontocetes were evident by healed lesions. Pilot whales and Risso's dolphins commonly interact with the pelagic longline fishery which operates throughout the western North Atlantic and elsewhere (Garrison, 2007). The presence of healed FI lesions on strandings indicates that some hooked animals survive. On the other hand, animals killed in the longline fishery with resulting fresh lesions are far from shore and unlikely to strand.

Table 6

Gear types found attached to or ingested by marine mammal strandings classified as HI-FI (human interaction evidence type is fishery interaction) (n=44) in North Carolina during 1997–2008. Seven animals were released alive. Research gear was set by the North Carolina Division of Marine Fisheries (NCDMF).

Species	Gear type	Ocean-side	In-shore	Live release
Balaenoptera edeni	line, trap or pot	1		
Megaptera novaeangliae	gill net	2		
Phoca vitulina	fishhook	1		
	gill net	3		1
Tursiops truncatus coastal	beach seine, multifilament research gear	1		
	beach seine, twine type unknown	1		1
	fishhook (ingested)	1		
	gill net	10	1	2
	gill net, beach-anchored	5		
	Gill net, research		1	
	line, monofilament and large hook	1		
	line, monofilament		2	
	line, monofilament-mixed	1		
	line, nylon with clear jug attached		1	1
	line, trap or pot		3	1
	line, thick multifilament—unknown source[1]		1	
	pound net		1	
	stop net	1		
	trawler, noncommercial	1		
Tursiops truncatus offshore	line, monofilament	1		
Unidentified balaenopterid	mixed-mutifilament webbing, rope, monofilament line, plastic bags	1		
Unidentified delphinid	line, polypropylene	1		
	line, trap or pot		1[2]	1
Unidentified odontocete	line, monofilament	1		
Total		33	11	7

[1] Line not recovered and source unknown, but animal had entanglement lesions consistent with webbing.
[2] Likely *Tursiops truncatus* coastal because occurrence was inshore.

All the pilot whales recovered with healed FI lesions occurred during a single stranding event and, thus, theoretically were from a single pod. Perhaps depredation of longline gear is a learned behavior that is confined within particular pods (Whitehead et al., 2004).

Baleen whales The overall presence of baleen whales primarily from winter through spring and their near absence during summer (May–September) align with known migration patterns (Rice, 1998). The most commonly stranded baleen whales were humpback and minke whales; these species may be more common in the stranding record because of their relative population abundance compared with that of other species of baleen whales, or they may be more common because of their distribution closer to shore (Waring et al., 2009b), or for both reasons. Humpback and minke whales were entirely represented by immature individuals, consistent with prior reports from New Jersey through Florida (Wiley et al., 1995). Wiley et al. (1995) suggested that some juvenile humpback whales may not migrate as far south as adults, but instead spend time feeding at mid-latitudes.

Along with vessel strikes, entanglement in fishing gear is a serious problem for large whales (Wiley et al., 1995; Kraus et al., 2005). The high rate of HI-FI strandings for humpback whales (10 of 23 or 43%) was higher than that reported during 1985–92 from New Jersey to Florida (5 of 20 or 25%) (Wiley et al., 1995). Humpback whales stranded in NC with fresh FI lesions were not necessarily entangled in gear set in NC because some whales carry entangling gear for an extended period of time before the entanglement potentially leads to the animal's death (Knowlton et al., 2012). Entanglement of whales has occurred, however, in gill nets set off NC. In one of these cases the whale died and later stranded. In the other case, the animal never stranded but instead breached, shook the net free, and was seen swimming without any gear at-

tached. Two of the stranded humpback whales showed evidence consistent with vessel strikes; one of these also had healed FI lesions (scars).

Coastal bottlenose dolphins Within the diversity of strandings, the most common species by far was the coastal bottlenose dolphin, which resides in coastal and inshore waters and is present all year. Interpretation of spatiotemporal patterns is complicated, however, because multiple stocks occur in NC waters, including at least 2 migratory coastal stocks and 2 resident estuarine stocks (Waring et al., 2010). These multiple stocks add to the regional biodiversity and influence seasonal local abundance. All 4 stocks are susceptible to incidental mortality in the myriad and seasonally changing commercial fisheries (Steve et al., 2001).

Stranding patterns tended to echo the spatiotemporal occurrence of commercial gillnet fisheries, the principal source of known fisheries bycatch for coastal bottlenose dolphins off NC (Waring et al., 2010). The annual decline in nonperinatal HI-FI bottlenose dolphin strandings likely represents a real decrease in bycatch due, in part, to a series of regulations on gillnet fisheries since 2000 (Federal Register, 2006; Byrd et al., 2008). The monthly patterns of HI-FI strandings were similar to those of effort in the gillnet fishery, which is greatest in spring and fall and lowest in summer (Steve et al., 2001). Although gill nets are used state-wide, the ocean fishery operates primarily from Oregon Inlet to Drum Inlet on the coast (from approximately ocean segments A2 to B1) (NCDMF[7]) and nearshore (0–5.6 km) (Palka and Rossman[8]). The concentration of strandings just south of Cape Hatteras may indicate higher bycatch rates in that area due to either higher local abundance of dolphins (Torres et al., 2005), greater concentrations of gillnet effort, or both. In some cases, carcasses from north of Cape Hatteras may be entrained in waters that are driven south around the cape during strong northeast winds, which are more typical during winter months than other seasons (Gray and Cerame-Vivas, 1963). Although overall seasonal effort in the inshore gillnet fishery is similar to that of the coastal fishery (Steve et al., 2001), the number of inshore strandings was too low to evaluate spatial effects.

The close alignment of the patterns of HI-CBD with HI-FI strandings among years, months, and coastal segments, and the absence of similar patterns for HI-no strandings, provides further evidence that a substantial portion of HI-CBD strandings may indeed be HI-FI. More evidence comes from animals that were CBD for FI, but were mutilated similarly to those known to be positive for FI. In addition, physical processes, such as winds and currents, that resulted in the deposition of HI-FI or HI-CBD animals should have the same effect on HI-no strandings; therefore, those processes are not likely to be causing the difference between HI-no and HI-CBD stranding patterns.

Although there was an annual decline in HI-no strandings, there were no month or spatial effects. A similar negative annual trend during 1992–2003 was not found in SC, an area that shares at least one bottlenose dolphin stock with NC (McFee and Hopkins-Murphy, 2002; McFee et al., 2006). Causes for the annual decline detected in this study are unknown. The lack of coastal segment or month effects was curious given the high seasonal variability in local abundance of coastal bottlenose dolphins along the NC coast, with more dolphins just south of Cape Hatteras in all seasons except summer (Torres et al., 2005; Waring et al., 2010). Changes in abundance, habitat shifts, or survivorship rates could have resulted in these patterns, but data do not exist to test these hypotheses.

Perinatal bottlenose dolphins were recovered in every month, although they were primarily bimodal with the spring mode more pronounced than the fall mode. This pattern is consistent with previous reports of neonate strandings in NC (Thayer et al., 2003) and SC (McFee et al., 2006). However, care should be taken when interpreting reproductive seasonality from stranded perinatal animals. On the basis of size alone, coastal bottlenose dolphins <125 cm could include calves up to 3 months of age (Fernandez and Hohn, 1998). Unfortunately, a standardized data collection to assess whether a small dolphin was a true neonate (*see* Thayer et al., 2003) has not been consistent. As a result, the presence of perinatal strandings in January, for example, does not necessarily mean that the dolphins were born in January. Also, it is possible that some of the smallest perinates were late-term aborted fetuses and their occurrence in the stranding record would influence interpretations of seasonality. Spatial patterns of perinatal strandings may result from differences in local abundance along the coast during calving season; however, fine-scale abundance or density estimates are not available.

Caveats on the use of stranding data as indicators of biodiversity and distribution

Marine mammal strandings can serve as indicators of biodiversity and spatiotemporal presence of live animals in nearby waters. Stranding data may also indicate changes in distribution, phenology, or mortality—sometimes before changes are detectable in source populations (Gulland, 2006). It is critical, therefore, to recognize the combination of stochastic and deterministic effects on the occurrence and discovery of stranded

[7] NCDMF (North Carolina Division of Marine Fisheries). 2007. Assessment of North Carolina commercial finfisheries, 2004–2007. Final performance report for NMFS award number NA 04 NMF4070216, 380 p. [Available from NCDMF, 3441 Arendell Street, Morehead City, NC 28557.]

[8] Palka, D. L., and M. C. Rossman. 2001. Bycatch estimates of coastal bottlenose dolphin *(Tursiops truncatus)* in U.S. mid-Atlantic gillnet fisheries for 1996–2000. U.S. Dep. of Commer., Northeast Fish. Sci. Cent. Ref. Doc. 01-15, 77 p. [Available from 166 Water Street, Woods Hole, MA 02543-1026 or http://nefsc.noaa.gov/nefsc/publications/crd/crd0115/0115.pdf, accessed June 2012.]

marine mammals in order for stranding data to serve as reliable proxies of those source populations.

Some degree of variability in the number of strandings is expected among years, months, and locations owing to the variety of factors that can affect the likelihood that an animal dying is beach-cast, or that carcasses persist on shore (without being washed out or buried by wave action) long enough to be observed, reported, and recovered. Winds and currents affect stranding rates (Peltier et al., 2012) and it would be interesting to investigate their influences on the patterns documented here. For example, southern NC had relatively few strandings, particularly of species other than coastal bottlenose dolphins. It is also farthest from the Gulf Stream and has a large estuary plume outflowing from the Cape Fear River (Xia et al., 2007), both of which likely impact stranding rates.

Increased mortality due to human interactions also affects stranding patterns. These effects are not always discernible because the ability to detect HI varies across the nature of the interaction. Evidence of fishery interactions, mutilation, vessel strikes, and gunshot wounds are relatively obvious to trained responders. In contrast, the detection of sonar effects on the presence and health of stranded marine mammals is challenging and requires a much more sophisticated sampling protocol than can be implemented for most strandings recovered in NC. The sampling protocol requires fresh carcasses, expertise of the responders, and availability of resources for histopathology analysis and computerized tomography (CT scanning) (*see* Cox et al., 2006). Insufficient data exist to comment on the prevalence of sonar exposure as a cause of strandings for the current study. Strandings positive for HI provide much needed information about the nature, timing, and frequency of interactions, especially in light of the limitations of fisheries observer programs to sufficiently cover all fisheries (Byrd et al., 2008). Although human interactions were detected in more than half of all species recovered (18 of 34), the number of strandings positive for HI was likely underestimated because of the relatively large number of strandings assigned to HI-CBD as result of decomposition, scavenger damage, and a conservative approach to assigning HI status. HI-no is the most difficult assignment to make. For example, strandings with questionable lesions would be assigned by default to HI-CBD.

Maintaining the quality and consistency of stranding data is not a simple task. The stranding network in NC, with its extensive coastline, relies heavily on public reporting and therefore ties to state, federal, and local municipalities have been key to receiving reports of, and in some cases gaining access to, strandings. The availability of trained participants to respond to stranding reports has also been vital to the collection of irreplaceable data and samples.

Conclusions

Marine mammal strandings in NC from 1997 to 2008 reflected the rich biodiversity occurring in waters off this unique location, where 'northern' and 'southern' species as well as coastal and pelagic species intersect. Therefore the spatial and temporal patterns detected from strandings can provide clues to the presence of living animals occurring off the NC coast. In some cases, those patterns reflect what is known from published records of aerial and shipboard surveys. For other species, little is known and stranding data serve as a proxy for live animal distribution. In addition, the detection of HI, particularly FI, provides crucial information on the spatiotemporal patterns and relative mortality levels from these interactions with marine mammals which are otherwise difficult to obtain *in situ* (Friedlaender et al., 2001; Byrd et al., 2008). Moreover, changes in stranding patterns can serve as indicators of underlying change in source populations due to anthropogenic or naturally occurring events.

Acknowledgments

The collection of stranding data requires assistance from many professionals and volunteers. We are grateful for their participation, particularly network contributors from the authors' institutions and the National Park Service, NC Division of Environment and Natural Resources, NC Division of Parks and Recreation, NC Maritime Museum, NC Sea Turtle Project, U.S. Coast Guard Sector NC, U.S. Fish and Wildlife Service, U.S. Marine Corps at Camp Lejeune, and municipalities in Carteret, Currituck, and Dare Counties. Statistical advice was provided by K. Shertzer (NMFS-Beaufort). The manuscript was improved by reviews of K. Craig (NMFS-Beaufort), S. Horstman (NMFS, Southeast Regional Office, St. Petersburg, FL), J. Litz (NMFS, Southeast Fisheries Science Center, Miami, FL), D. A. Pabst (University of North Carolina Wilmington, Wilmington, NC), K. Shertzer, and 3 anonymous reviewers. Stranding response was authorized by the NMFS pursuant to Sections 109(h) and 112(c) of the Marine Mammal Protection Act.

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Population genetics of Cobia (*Rachycentron canadum*): implications for fishery management along the coast of the southeastern United States

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Abstract—Cobia (*Rachycentron canadum*) is a pelagic, migratory species with a transoceanic distribution in tropical and subtropical waters. Recreational fishing pressure on Cobia in the United States has increased substantially during the last decade, especially in areas of its annual inshore aggregations, making this species potentially susceptible to overfishing. Although Cobia along the Atlantic and Gulf coasts of the southeastern United States are currently managed as a single fishery, the genetic composition of Cobias in these areas is unclear. On the basis of a robust microsatellite data set from collections along the U.S. Atlantic coast (2008–09), offshore groups were genetically homogenous. However, the 2 sampled inshore aggregations (South Carolina and Virginia) were genetically distinct from each other, as well as from the offshore group. The recapture of stocked fish within their release estuary 2 years after release indicates that some degree of estuarine fidelity occurs within these inshore aggregations and supports the detection of their unique genetic structure at the population level. These results complement the observed high site fidelity of Cobias in South Carolina and support a recent study that confirms that Cobia spawn in the inshore aggregations. Our increased understanding of Cobia life history will be beneficial for determining the appropriate scale of fishery management for Cobia.

Manuscript submitted 25 April 2012.
Manuscript accepted 6 November 2013.
Fish. Bull. 112:24–35 (2014).
doi: 10.7755/FB.112.1.2

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necesarily reflect the position of the National Marine Fisheries Service, NOAA.

Cobia (*Rachycentron canadum*), belonging to the monotypic family Rachycentridae (Actinopterygii: Perciformes), is a large, pelagic, migratory species distributed throughout tropical and subtropical waters of the Atlantic, Indian, and western Pacific oceans (Shaffer and Nakamura, 1989). The species is highly prized by both recreational fisheries and aquaculture producers as excellent table fare. Within the United States, this recreationally and commercially important fish species occurs along the southeastern Atlantic and Gulf of Mexico coasts. Cobia has historically been managed by the South Atlantic Fishery Management Council and Gulf of Mexico Fishery Management Council as a single reproductive stock on the basis of minimal data from tag and recapture research and mitochondrial fragment analysis (Hrincevich, 1993). Most early life history information on Cobia comes from aquaculture research, and little is known about its natural life history.

In the spring and early summer months, Cobias in the western North Atlantic are thought to migrate with warming waters from Florida to the Chesapeake Bay (Shaffer and Nakamura, 1989). During this putative northward migration, Cobias enter high salinity bays and estuaries, including Port Royal Sound and St. Helena Sound in South Carolina (SC), Pamlico Sound in North Carolina (NC; Smith, 1995), and the Chesapeake Bay (Shaffer and Nakamura, 1989). Cobias have been reported to spawn from April to September (Smith, 1995; Lotz et al., 1996; Burns et al.;[1] Brown-Peterson et al., 2001). Regional peaks in spawning correlate with their proposed annual migration from Florida to Massachusetts, occurring in May along the SC coast (Shaffer and Nakamura, 1989; Burns et al.[1]), June in NC (Smith, 1995), and during June and July in the Chesapeake Bay region (Joseph et al., 1964).

One aspect of Cobia biology that has only recently been investigated is their annual inshore aggregations that occur in high-salinity estuaries. The nature of these aggregations has been hypothesized to be associated with either feeding or reproduction (Joseph et al., 1964; Richards, 1967; Hassler and Rainville, 1975; Smith, 1995; Lotz et al., 1996; Burns et al.[1]),

[1] Burns, K., C. Neidig, J. Lotz, and R. Overstreet. 1998. Cobia (*Rachycentron canadum*) stock assessment study in the Gulf of Mexico and in the south Atlantic. Mote Marine Laboratory Technical Report No. 571, 108 p. [Available from Mote Marine Laboratory, 1600 Thompson Parkway, Sarasota, FL 342236.]

and only recently has research verified the reproductive function of these aggregations through documentation of the presence of eggs, newly hatched Cobia larvae and reproductively mature females within the Port Royal Sound and St. Helena Sound estuaries in SC (Lefebvre and Denson, 2012). Therefore, the limited understanding of Cobia life history provides conflicting expectations regarding the genetic structure at the population level (hereafter 'population genetic structure'). On one hand, their pelagic nature and transoceanic distribution would indicate a high potential for long distance movement and gene flow (i.e., no genetic structure expected); conversely, the presence of site-specific spawning aggregations might indicate a low potential for gene flow (i.e., genetic structure expected). Because the foundation for effective management of marine fishes is built upon the determination of biological population segments, a better understanding of Cobia biology and population genetic structure over a broad geographic area is necessary.

Commercial and recreational U.S. harvests of Cobia along the middle and south Atlantic have been highly variable over time, but generally have been increasing since 1980 (Atlantic Coastal Cooperative Statistics Program, http://www.ACCSP.org). Concurrently, recreational fishing pressure on Cobias has increased substantially in the last decade, especially in areas where they exhibit annual inshore aggregations (SC, VA) and this pressure has made them susceptible to overfishing during a potentially critical life stage. In these areas, fishing tournaments focused solely on Cobias are popular (McGlade, 2007) and "catch and release" is the exception rather than the rule. Therefore, with continued increases in human populations in coastal areas and subsequent increased fishing pressure on both offshore and inshore coastal finfish populations, the South Carolina Department of Natural Resources (SCDNR) began evaluating the feasibility of stocking Cobias as a management option. In 2001, the SCDNR began collecting Cobias from the wild, developing broodstock conditioning regimes, spawning broodstock in the laboratory, and producing juveniles for aquaculture development and stock enhancement (Weirich et al., 2004). In addition, efforts were made to collect life history information (spawning, growth, and genetics) of the wild populations during seasonal migrations. Externally tagged, cultured fish were also released into the estuary from which the wild broodstock had been collected as a fisheries research tool to monitor movement, determine appropriate tag types, identify site fidelity, determine growth rates, and verify annulus formation in otoliths.

In 2007, shortly after Pruett et al. (2005) and Renshaw et al. (2006) published microsatellite loci for Cobia, we optimized 3 multiplexed microsatellite panels of 10 loci to use as genetic tags for stocked fish and population genetic analyses. Although the genetic tools were not ready for use until 2007, fin clips were available from all hatchery broodstock used in the program between 2004 and 2007. Here, we present population genetic data on the basis of the 2008 and 2009 collections and recapture data for Cobias collected from south Atlantic coastal waters. Specifically, our goals are to characterize the genetic structure of the Cobia population along the southeast Atlantic coast of the United States; determine if population genetic structure is detectable on the basis of movement patterns; document if any degree of estuarine fidelity occurs in Cobias; and evaluate whether genetic data support the reproductive role of their seasonal inshore aggregations. Because of the general lack of knowledge of their biology, we used a multidisciplinary effort over a broad geographical area to address current obstacles facing management of Cobia.

Materials and methods

Broodstock and production

Broodstock used for the production of all stocked fish was collected from the Port Royal Sound estuary (Fig. 1); the broodstock pool ranged from 9 to 16 individuals per year (Table 1). Spawning occurred at the Marine Resources Research Institute in Charleston, SC, and Waddell Mariculture Center in Bluffton, SC, and all rearing occurred in outdoor nursery ponds at the Waddell Mariculture Center. Relatively small numbers of fish have been produced and released since 2004; 2007 represented the largest release with ~54,000 fish (Table 1). All year classes are identifiable with distinct genetic tags (as described later). Genetic tags offer a noninvasive, permanent approach that can be applied to all sizes of fish, including larvae, and they are identifiable through parentage analysis. Small juveniles were released at approximately 30 days after hatching, large juveniles at approximately 90 days after hatching, and yearlings the following spring. Yearlings from the 2004 and 2005 year classes were also individually tagged with external tags before release. Either an 89-mm or 127-mm nylon dart tag (Hallprint Pty Ltd.,[2] Hindmarsh Valley, Australia) was inserted into the dorsal musculature. All Cobia releases occurred in the Port Royal Sound at the Trask boat landing in Bluffton, SC.

Sampling

Anal-fin tissue samples were collected from adult Cobias at fishing tournaments, filleted fish carcasses donated to SCDNR's freezer program by cooperating anglers, and fish collected by SCDNR personnel during the spawning seasons of 2008 and 2009 (April–July). Because Cobia is a federally managed species with a minimum size limit of 83.8 cm fork length (~93.8 cm TL), the species is not expected to recruit to the fishing

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

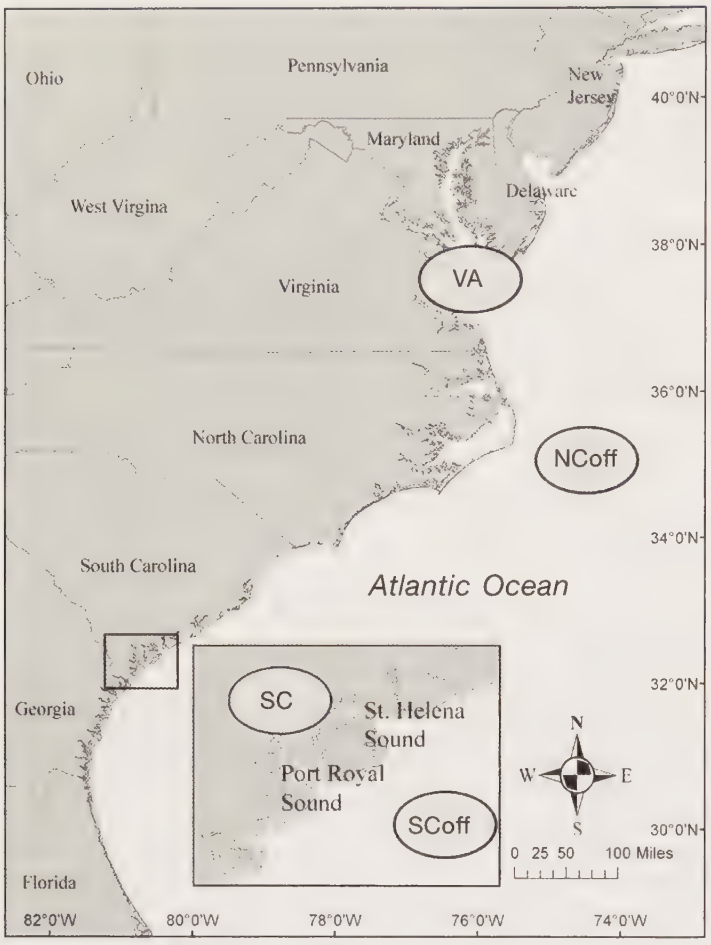

Figure 1

Map of sampling locations for Cobias (*Rachycentron canadum*) from 2008 to 2009 along the Atlantic coast of the southeastern United States. Locations included inshore Virginia (VA), offshore North Carolina (NC_{Off}), inshore South Carolina (SC), and offshore South Carolina (SC_{Off}).

gear until 2–3 years of age, thus creating a potential lag in recruitment and subsequent genetic identification of up to 3 years. Collection locations were provided for each specimen by participating anglers. Our 2008 collection comprised a broader geographic scope than that of 2009. In 2008, we obtained 488 samples from Virginia (VA), NC, and SC; whereas, our 2009 collection comprised 290 samples from only NC and SC. Although our SC-collected sample sizes were high in both years (349 and 234), specific capture location details were missing from the associated collection data for many samples. As described later, samples were included in each analysis only if appropriate associated data were available (Table 2). Collections during both years were confined to limited areas; the southern portion of the state of SC, the offshore area of the Albemarle Sound in NC, and the vicinity of Chesapeake Bay in VA (Fig. 1). Collected fin tissue was stored at room temperature in a solution for the stabilization of DNA and cell lysis—a solution made of 8 M urea, 1% sarkosyl, 20 mM sodium phosphate, and 1 mM EDTA. Externally tagged Cobia were recaptured during the previously described sample collections as well as through additional tag reporting by recreational anglers during both years.

Molecular protocols

Total DNA was isolated from the sarkosyl-urea solution and tissue lysate by using the Agencourt SprintPrep plasmid purification system (Beckman Coulter, Inc., Brea, MA) according to the manufacturer's instructions. Ten microsatellite loci were amplified in 3 multiplexed polymerase chain reactions. Each reaction contained 0.2 mM dNTPs, 1×HotMaster buffer with 2.5 mM Mg^{2+}, 0.025 units Hotmaster *Taq* DNA Polymerase (5 Prime, Inc., Gaithersburg, MD), and 0.5 mM $MgCl_2$, 0.20 mg/mL BSA, 0.3 µM forward and reverse primers, and 1 µL of 1:10 diluted DNA isolate. All forward primers were labeled with WellRED florescent dyes (Beckman Coulter, Inc.); individual primer concentrations differed for each locus (Table 3). All amplifications were performed in 11-µL reaction volumes in iCycler systems (Bio-Rad Laboratories, Hercules, CA) by using a 60°C touchdown protocol (modified from Renshaw et al., 2006) that consisted of 3 steps after initial denaturation at 94°C for 2 min. Step 1 included 7 cycles of 94°C for 30 s, 60°C for 1 min and 64°C for 2 min. Step 2 included 7 cycles of 94°C for 30 s, 57°C for 1 min and 64°C for 2 min. Step 3 included twenty cycles of 94°C for 30 s, 54°C for 1 min and 64°C for 2 min, followed by a final extension at 64°C for 60 min. The protocol includes substantial decreases in extension times from that of Renshaw et al. (2006) to shorten the overall length of the protocol. All amplifications were run with 2 negative controls. Reaction products and size standards (GenomeLab DNA Size standard Kit 400; Beckman Coulter, Inc.) were separated with a CEQ8000 automated DNA sequencer (Beckman Coulter, Inc.), and fragment size analysis was performed with the CEQ8000 software package. All chromatograms were scored manually, and genotypes were verified independently by a second reader. Approximately 10% of the samples were regenotyped to provide validation.

Marker statistics and parentage analysis

The sample data pooled over collection years were used to test all loci for adherence to Hardy-Weinberg equilibrium (HWE), linkage disequilibrium, and the presence of genotyping artifacts at each collection locality separately (i.e., for SC samples, only those with known collection information were included). Examinations for departures from HWE and for linkage disequilibrium between loci pairs were performed in the program Ar-

Table 1

Summary of data for tagged and released cultured Cobia (*Rachycentron canadum*) in South Carolina by release year, with number of broodstock used for production, size at release, mean total length (TL), and number of individuals released. Small juveniles were released during the summer of the production year, large juveniles were released during the fall of the production year, and yearlings were released the following spring.

Year class	Number of broodstock	Size at release	Mean TL (mm)	Number released
2004	8	Small juveniles	97	1128
		Large juveniles	328	679
		Yearlings	496	93
2005	7	Small juveniles	56	3200
		Large juveniles	230	516
		Yearlings	545	385
2007	16	Small juveniles	82	53,264
		Large juveniles	250	409
		Yearlings	541	59
2008	11	Large juveniles	249	2000
		Yearlings	530	54
2009	9	Large juveniles	235	1392

lequin 3.11 (Excoffier et al., 2005) with default parameters. The frequencies of potential null alleles at each locus were estimated in Cervus, vers. 3.0 (Kalinowski et al., 2007). Significance levels for all simultaneous analyses were adjusted with a sequential Bonferroni correction (Rice, 1989).

To confirm the utility of the marker suite for genetic evaluation and parentage analysis (i.e., identification of genetic tags), loci were examined for genetic diversity and polymorphism, for the ability to distinguish between related individuals, and for adherence to the principles of Mendelian inheritance. Basic molecular diversity indices, including number of alleles per locus (N_a), and allelic size range were calculated for each locus through the use of Arlequin software. Cervus was used to estimate the average parent-pair and identify nonexclusion probabilities for the loci suite—indices that measure the probability that a set of markers will match erroneous parents to offspring and the probability that a set of markers will not be able to distinguish between related individuals, respectively.

To determine whether hatchery individuals contributed to the southeastern Atlantic Cobia populations, parentage analyses were conducted that incorporated all field samples and hatchery broodstock. Simulations (n=5) for the "sexes known" parentage analysis in Cervus consisted of 10,000 offspring and 8 candidate parent pairs per year (100% sampled) with allele frequencies generated from all Cobia samples. Critical delta values were determined with 95% confidence for the relaxed criteria and with 99% confidence for the strict criteria. All parentage analyses were run with the modal simulation file. Although all project samples genotyped at 8 or more loci were subjected to parentage analyses, contribution calculations were limited to only those sampled within the stocking area. The percentage of hatchery contribution is reported as $[S(W+S)^{-1}]100$, where S is the number of stocked individuals and W is the number of wild individuals as designated by Cervus at the strict confidence level because no additional offspring were identified with the relaxed criteria. Contribution is reported in terms of both population (all samples) and year class (on the basis of known-age fish). All sampled fish identified as being of hatchery origin were removed from population structure analyses. Identity analyses (as implemented in Cervus) were also conducted to compare the 2008 and 2009 samples in order to identify recaptures of both hatchery and wild individuals.

For the Mendelian inheritance tests, 25 offspring from two parental families of the 2007 hatchery production year were compared with the 2007 broodstock by using Probmax, vers. 3.1 parentage analysis software (Danzmann, 1997) to verify the contributing parent pairs. The genotypes of the contributing parents were merged into a single file and imported into FAP 3.6 (Taggart, 2007), to generate all the possible progeny genotypes associated with these parental crosses. A chi-square analysis (χ^2) was performed to compare the observed genotypic frequencies from the progeny data set with the expected genotypic frequencies from FAP.

Population genetic analyses

For all population genetic analyses, samples were partitioned into those from the inshore aggregations (defined as being captured landward of the barrier island, either along the coast or in the estuary) and

Table 2

Distribution of Cobia (*Rachycentron canadum*) collected during 2008 and 2009 with a known collection location that were included in the analyses of population genetic structure. Dashes indicate locations where no sampling occurred.

Location	2008	2009
Virginia inshore	35	–
North Carolina offshore	90	56
South Carolina inshore	103	109
South Carolina offshore	71	55

Table 3

Multiplex group (panel), locus, fluorescent label (dye), repeat motif, and primer concentrations (μM) for polymerase chain reactions for 10 Cobia-specific microsatellite loci (modified from Renshaw et al., 2006). Summary statistics for each locus were based on the total combined project data set. n=sample size, N_A= number of alleles, A=allelic size range.

Panel	Locus	WellRED dye	Repeat motif	[Primer]	n	N_A	A
1	Rca1-H10	D2	CA	0.10	514	11	116–138
	Rca1-A04	D4	$(CA)_9(CACT)_4$	0.05	516	11	180–210
	Rca1B-E02	D4	CT	0.15	516	7	301–317
2	Rca1-A11	D4	GT	0.05	513	22	166–212
	Rca1B-H09	D2	GATA	0.09	516	17	169–233
	Rca1B-E08A	D3	CA	0.11	516	12	201–247
	Rca1B-C06	D4	GATA	0.05	514	22	329–417
3	Rca1B-D10	D3	CTAT	0.13	515	28	132–260
	Rca1-E11	D2	CA	0.04	518	6	167–181
	Rca1-C04	D4	GT	0.13	516	17	221–261

those from offshore areas (defined as captured seaward of the barrier islands, mostly near wrecks or reefs); samples without sufficient collection details for assignment were excluded (Table 2). Samples collected from the Port Royal Sound and St. Helena Sound estuaries were pooled for the SC inshore location because tagged fish recaptured after being at liberty for only a short period indicated substantial movement between these adjacent and connected estuaries.

An exact G-test with Markov Chain permutations, as implemented in Genepop, vers. 4.0.10 (Raymond and Rousset, 1995), was used to test for pairwise differences in genotypic distributions among collection locations during each collection year. Markov chain parameters included 10,000 dememorizations, 100 batches, and 5000 iterations per batch. Part of the analyses of genetic structure used R_{ST} statistics, which incorporate a stepwise mutation model to estimate population differentiation and are analogous to F_{ST} statistics (Slatkin, 1995). Pairwise, hierarchical R_{ST} statistics were calculated and an analysis of molecular variance (AMOVA) was conducted—as implemented in Arlequin with 10,000 iterations to determine the degree of genetic structuring occurring among states. Structure, vers. 2.3 (Pritchard et al., 2000) also was used to infer subpopulations through a clustering-based algorithm. The Admixture with LocPrior model was implemented, including runs of k=1–4 for the 2008 collection and k=1–3 for the 2009 collection. All models incorporated 10,000 iterations and a 10,000 burn-in period and were replicated in triplicate. Pairwise comparisons of genotypic distributions and R_{ST} calculations between 2008 and 2009 collection locations were conducted as described previously to determine the degree of temporal genetic stability of Cobia populations along the southeastern U.S. Atlantic coast as well as to validate temporal pooling of samples for genetic characterization of detected populations. Populations were characterized genetically by calculation of the average number of alleles per locus (N_a), observed heterozygosity (H_O), genetic diversity (H_E; Nei, 1987), and inbreeding coefficients (F_{IS}) by using Arlequin and Genepop.

Results

For this project, 764 individuals were genotyped. For both collection years, high proportions of loci were able to be scored unambiguously with high repeatability (>99%), resulting in low levels of missing data (2008: 1.6%; 2009: 0%). Genetic data from 519 samples were used for all loci testing (Table 2). All loci at all collection locations were found to be in HWE (P>0.05), with no evidence of null alleles (frequency<0.06) and no indication of linkage disequilibrium between any loci (critical P-value after Bonferonni=0.001). All 10 loci were polymorphic with allelic richness ranging from 6 to 28 (mean: 15.4 alleles per locus) (Table 3). The χ^2 test for comparing hatchery broodstock and offspring indicated that all loci are inherited in a Mendelian fashion (Table 4).

The loci suite provides an average nonexclusion parent-pair probability of 1.3×10^{-7} and average nonexclusion identity probability of 5.8×10^{-12}, signifying that the possibility of misassignment of parentage in the parentage analysis is substantially less than 0.01% and individuals can be identified confidently. Therefore, on the basis of initial tests, our suite of microsatellite markers is valuable for characterization of population genetic diversity and genetic structure, as well as for parentage analysis because the loci are genetically

Table 4

Mendelian inheritance statistics for two independent families of Cobia (*Rachycentron canadum*): chi-square (χ^2) values, degrees of freedom (df), and *P*-values at each of the 10 Cobia-specific microsatellite loci. For two loci in family 2, both parents were homozygous for different alleles and all offspring were fixed heterozygotes, as expected (an asterisk indicates each of these loci).

	Family 1			Family 2		
Locus	χ^2	df	*P*-value	χ^2	df	*P*-value
Rca1-H10	2.27	1	0.131	1.33	1	0.248
Rca1-A04	0.09	1	0.764	0.50	2	0.778
Rca1B-E02	2.27	1	0.131	0.00	1	1.000
Rca1-A11	4.40	3	0.221	1.00	1	0.317
Rca1B-H09	0.00	1	1.000	5.33	2	0.069
Rca1B-E08A	1.80	2	0.406	*	–	–
Rca1B-C06	3.00	3	0.391	2.45	3	0.484
Rca1B-D10	1.00	3	0.801	0.40	1	0.527
Rca1-E11	1.22	2	0.543	*	–	–
Rca1-C04	0.00	1	1.000	3.89	3	0.273

varied, adhere to the expectations of Mendelian inheritance, distinguish between related individuals, and correctly match offspring to their parents with a high degree of confidence.

Movement and estuarine fidelity

No fish collected outside of SC were genetically identified as SC-stocked fish; therefore our evaluation of hatchery contribution represents their contribution to SC Cobia populations. Parentage analysis of 341 samples identified two fish in the SC 2008 collections that were both originally stocked in 2004 into Port Royal Sound. On the basis of otolith aging, 174 fish from the 2004 year class (YC) were present in the SC 2008 collections. Therefore, the 2004 stocked fish made a 1.1% contribution to the SC 2004 YC of Cobias. A large number of the SC 2008 samples, including the two recaptured stocked fish, were missing specific collection details. Without these details, we were unable to assign samples to inshore and offshore groups. Therefore, the year-class contribution was estimated on the basis of all SC samples—an assessment that likely underestimated the true contribution. From the 2008 samples, the 2004 YC stocked fish represented 0.6% of all SC-collected samples.

From the 2009 collections (n=232), 11 stocked fish were identified, all from the 2007 YC small juvenile stockings in Port Royal Sound. Thirteen 2007 YC fish were identified in the 2009 collections, resulting in an 84.6% contribution of stocked fish to the SC Cobia 2007 YC and a 4.7% contribution to the overall SC population of sampled Cobias. Of the identified stocked fish, 8 were recaptured within the Port Royal Sound estuary, and the remaining 3 recaptured stocked fish did not have sufficient collection information for group assignment. In addition to the recapture of stocked fish in their release estuary, one wild fish was recaptured within the Port Royal Sound estuary in multiple years (this finding was based on genetic identity analyses—see previous section). No wild recaptures were detected among different collection locations. Although these recaptures were represented by low sample sizes, the pattern of site fidelity among all recapture groups was consistent.

For external tag recaptures, 7 tag returns were reported from the 2004 YC of stocked yearling Cobias (93 originally stocked; Table 5). Within 32 days after release (mean of 25 days at large), 5 of the fish were recaptured, and 1 fish was recaptured later that summer; however, the remaining fish was recaptured the following spring after 370 days at large. All tag returns of 2004 YC fish were recaptured within the SC inshore area. From the 2005 YC fish that were stocked with external tags (n=385), 58 were recaptured over a 3-year period. Two of these recaptures were reported with no collection information. Within 40 days after release (mean of 17 days at large), 44 of the 2005 YC fish were recaptured, and all of the fish that were reported with location information were recaptured within the SC inshore area. Of the remaining fish, 7 were recaptured within the SC inshore area 2–3 years after their stocking during the spawning season; these fish had a mean of 813 days at large. The final 5 fish were recaptured

Table 5

Summary of recapture information for Cobia (*Rachycentron canadum*) released in South Carolina with external tags. Distance values represent the distance from the specific stocking location in Port Royal Sound to the recapture location. Calibogue Sound is a small estuary in the vicinity of Port Royal Sound and St. Helena Sound estuaries in South Carolina (SC).

Year class	Tag no.	Release date	Recapture date	Recapture location	Days at large	Distance (km)
2004	M0562	05/11/05	05/27/05	Port Royal Sound	16	–
2004	M1472	05/11/05	05/28/05	Port Royal Sound	17	10.0
2004	M1382	05/11/05	06/09/05	Port Royal Sound	29	10.0
2004	M1397	05/11/05	06/09/05	Port Royal Sound	29	10.0
2004	M1434	05/11/05	06/12/05	Port Royal Sound	32	–
2004	M1477	05/11/05	08/25/05	Port Royal Sound	106	11.6
2004	M1326	05/11/05	05/16/06	Port Royal Sound	370	–
2005	M2079	05/03/06	05/07/06	Port Royal Sound	4	0.0
2005	M2245	04/27/06	05/02/06	Port Royal Sound	5	12.2
2005	M2082	05/03/06	05/10/06	Port Royal Sound	7	11.0
2005	M2357	05/03/06	05/10/06	Port Royal Sound	7	11.0
2005	M2360	05/03/06	05/10/06	Port Royal Sound	7	10.0
2005	M2327	05/08/06	05/16/06	Port Royal Sound	8	10.0
2005	M2282	04/27/06	05/06/06	Port Royal Sound	9	10.0
2005	M2081	05/03/06	05/12/06	Port Royal Sound	9	9.3
2005	M2227	05/03/06	05/12/06	Port Royal Sound	9	12.2
2005	M2310	05/08/06	05/17/06	–	9	–
2005	M2089	05/03/06	05/13/06	Port Royal Sound	10	11.0
2005	M2234	04/27/06	05/08/06	Port Royal Sound	11	11.0
2005	M2239	04/27/06	05/08/06	–	11	–
2005	M2321	05/08/06	05/20/06	Port Royal Sound	12	10.0
2005	M2018	04/27/06	05/10/06	Port Royal Sound	13	0.0
2005	M2091	05/03/06	05/17/06	Port Royal Sound	14	11.0
2005	M2132	05/03/06	05/17/06	Port Royal Sound	14	–
2005	M2155	05/03/06	05/17/06	Port Royal Sound	14	11.0
2005	M2205	05/03/06	05/17/06	Port Royal Sound	14	10.0
2005	M2285	05/08/06	05/22/06	Port Royal Sound	14	11.0
2005	M2024	04/27/06	05/12/06	Port Royal Sound	15	10.0
2005	M2210	05/03/06	05/19/06	Port Royal Sound	16	11.0

outside of the stocked area (3 in SC and 2 in Florida); however, these fish were recaptured either outside of the spawning season (September–October) or just before or at the onset of the spawning season (early May). Although the sample sizes for recaptures at large for at least one year were small (n=13), all of the recaptures during the spawning season (n=8) occurred within the inshore vicinity of the stocked estuary.

Population structure

On the basis of the 2008 samples, pairwise comparisons of both genotypic distributions and hierarchical R_{ST} values indicated no differences among the offshore collection locations (G-test: P=0.075, R_{ST}=0.005, P=0.14; Table 6). However, the two inshore collection locations were significantly different from both each other (G-test: P<0.001; R_{ST}: 0.043, P<0.001) and from the homogenous offshore group (G-test: P<0.001; R_{ST}: 0.011–0.023, P<0.05); with the exception of the inshore VA and offshore NC collection locations. The AMOVA results were consistent with this pattern, showing significant differences among populations (1.6%, P<0.001, Table 7) and the highest proportion of among-group molecular variation (1.3%) when grouped according to the pair-wise results. Results derived from the 2009 samples were concordant with the patterns detected in 2008 (AMOVA: 1.2%, P<0.001; 2.3% among groups), with the SC inshore collection being significantly different (G-test: P<0.001; R_{ST}: 0.017–0.018, P<0.009) from the homogenous NC and SC offshore group (G-test: P=0.53; R_{ST}=0.006, P=0.16; Table 8). Results from use of the Structure software for both collection years supported the pairwise and AMOVA patterns of genetic differentiation (Fig. 2). On the basis of trajectories of both Ln probabilities and variance metrics, k (number of populations) was estimated at 3 populations for the 2008

Table 5 (*continued*)

2005	M2211	05/03/06	05/19/06	Port Royal Sound	16	11.0
2005	M2028	04/27/06	05/14/06	St. Helena Sound	17	62.0
2005	M2102	05/03/06	05/20/06	–	17	–
2005	M2086	05/03/06	05/21/06	Port Royal Sound	18	11.0
2005	M2107	05/03/06	05/21/06	Port Royal Sound	18	11.0
2005	M2146	05/03/06	05/21/06	Port Royal Sound	18	11.0
2005	M2007	04/27/06	05/16/06	Port Royal Sound	19	11.0
2005	M2187	05/03/06	05/22/06	Port Royal Sound	19	11.0
2005	M2005	04/27/06	05/17/06	Port Royal Sound	20	11.0
2005	M2042	04/27/06	05/17/06	Port Royal Sound	20	11.0
2005	M2002	04/27/06	05/19/06	Port Royal Sound	22	11.0
2005	M2232	04/27/06	05/19/06	Port Royal Sound	22	11.0
2005	M2016	04/27/06	05/21/06	Port Royal Sound	24	–
2005	M2039	04/27/06	05/21/06	Port Royal Sound	24	–
2005	M2163	05/03/06	05/29/06	–	26	–
2005	M2223	05/03/06	05/29/06	–	26	–
2005	M2241	04/27/06	05/24/06	Port Royal Sound	27	–
2005	M2068	05/03/06	06/05/06	–	33	–
2005	M2141	05/03/06	06/05/06	St. Helena Sound	33	54.7
2005	M2015	04/27/06	06/02/06	Port Royal Sound	36	11.0
2005	M2027	04/27/06	06/02/06	Port Royal Sound	36	11.0
2005	M2242	04/27/06	06/06/06	Port Royal Sound	40	11.0
2005	M2377	05/03/06	05/05/07	Charleston Harbor	367	123.9
2005	M2249	05/03/06	09/15/07	Offshore SC	500	65.5
2005	M2131	05/03/06	05/20/08	Port Royal Sound	748	11.0
2005	M2238	04/27/06	05/20/08	Calibogue Sound	754	44.3
2005	M2017	04/27/06	05/25/08	Port Royal Sound	759	20.6
2005	M2281	04/27/06	05/30/08	Port Royal Sound	764	11.0
2005	M217?	05/03/06	06/18/08	Port Royal Sound	777	20.0
2005	M2046	04/27/06	06/18/08	Port Royal Sound	783	20.0
2005	M2197	05/03/06	10/03/08	Offshore SC	884	77.2
2005	M2118	05/03/06	05/11/09	Offshore FL	1104	241.4
2005	M2387	05/03/06	05/15/09	Port Royal Sound	1108	11.0
2005	M2265	05/03/06	09/14/09	St. Mary's River, FL	1230	207.6
2005	M2004	04/27/06	–	–	–	–
2005	M2051	05/03/06	–	–	–	–

Table 6

Summary of results for the comparision of genotypic distribution (*P*-values below diagonal) and R_{ST} pairwise (above diagonal) location from the 2008 sample collections of Cobia (*Rachycentron canadum*). Collection locations included inshore Virginia (VA), offshore North Carolina (NC_{Off}), and offshore South Carolina (SC_{Off}), and inshore South Carolina (SC). Bold type indicates statistical significance after Bonferroni correction (critical P=0.008).

	VA	NC_{Off}	SC_{Off}	SC
VA	–	0.001	**0.011**	**0.043**
NC_{Off}	0.013	–	0.005	**0.023**
SC_{Off}	**<0.001**	0.075	–	**0.016**
SC	**<0.001**	**<0.001**	**<0.001**	–

collection and 2 populations for the 2009 collections. Consistent with the low R_{ST} estimates, the results from the Structure software indicated the presence of mixed ancestry among these populations.

Temporal within-location comparisons of the 2008 and 2009 collections showed no significant differences in genetic compositions (G-test: P=0.51–0.56; R_{ST}<0.006, P>0.016), validating the pooling of samples across collection years for population characterization. Basic molecular diversity indices were similar among collection locations, with high levels of genetic diversity across all loci and high levels of polymorphism (Table 9). The mean number of alleles per locus ranged from 10.4 to 14.0 (average allelic range: 14.5–16.4). The overall average observed heterozygosity for Cobias was moderate and ranged from 0.709 in the SC inshore collection to 0.772 in the VA inshore collection, with the NC and SC offshore collections showing intermediate

Table 7

Summary of analysis of molecular variance (AMOVA) indicating partitioning of genetic variation on the basis of our 2008 (top) and 2009 (bottom) sample collections of Cobia (*Rachycentron canadum*) in South Carolina. df=degrees of freedom.

Collection year	Source of variation	df	Sum of squares	Variance component	Percentage of variation	*P*-value
2008	Among populations	3	973	1.6	1.6	<0.0001
	Within populations	594	56,980	95.9	98.4	
	Total	597	57,953	97.5		
2009	Among populations	2	473	1.1	1.2	<0.0001
	Within populations	437	37,760	86.4	98.8	
	Total	439	38,233	87.5		

diversity. Inbreeding was low (P>0.21; F_{IS}<0.07) in all collection locations.

Discussion

In recent years, SCDNR has expanded the use of genetic tools to identify many types of stocked fish, specifically Red Drum (*Sciaenops ocellatus*), Striped Bass (*Morone saxatilis*), and Spotted Seatrout (*Cynoscion nebulosus*), and to characterize their genetic population structure. These tools create permanently identifiable tags with the use of microsatellite markers that are useful for genetically characterizing fish populations. South Carolina's Cobia research program is the first to begin rigorously evaluating U.S. populations from a genetic perspective. On the basis of our U.S. collections of Cobias encountered along the south Atlantic coast, tests of both genotypic distributions and pairwise hierarchical R_{ST} statistics indicate that the offshore groups are genetically homogenous, a finding that is consistent with Hrincevich's (1993) findings. However, the detection of the two genetically distinct inshore aggregations (SC and VA) is new information in our understanding of Cobia life history. Although a significant degree of genetic isolation was detected among these inshore aggregations and the offshore group, the low R_{ST} statistics and the mixed ancestry patterns indicate that a low level of gene flow does occur.

Table 8

Results of the genotypic distribution (*P*-values below diagonal) and R_{ST} pair-wise (above diagonal) comparisons of locations from the 2009 sample collections of Cobia (*Rachycentron canadum*). Collection locations were offshore North Carolina (NC_{Off}), offshore South Carolina (SC_{Off}), and inshore South Carolina (SC). Bold type indicates statistical significance following Bonferroni correction (critical P=0.017).

	NC_{Off}	SC_{Off}	SC
NC_{Off}	–	0.006	**0.017**
SC_{Off}	0.529	–	**0.018**
SC	**<0.001**	**<0.001**	–

We recognize that population structure can be easily masked by a mixed stock effect, whereby gene flow is limited among population groups by different spawning behaviors, yet intermingling occurs outside of the spawning period. For example, if populations of fish spawn in unique locations but intermingle and migrate with other populations during the nonspawning season, the composition of nonspawning breeding stocks would appear to be homogenous in terms of allele frequency distributions, whereas gene flow would be restricted to individuals spawning at each unique spawning site. Only sampling of spawning individuals at each unique spawning site would reveal the true genetic structure. Although we have temporally limited our sampling to the spawning period of Cobia, it is possible that the lack of detected genetic differences between the VA inshore aggregation and the NC offshore samples is due to confounding effects of the potential migration patterns of Cobia. In a migrating species, the logistics of sampling individuals in one location without resampling from the same group in another location is challenging. Although temporally limiting sampling can lessen the confounding effects of such migrations on evaluations of population genetics, in the case of Cobias, the limited period of accessibility for sampling coincides with both their spawning season as well as their proposed northward migration. Therefore, although our sampling was temporally limited, it is possible that VA individuals were present among the Cobias collected offshore of NC as they were completing their migration to the VA inshore aggregation.

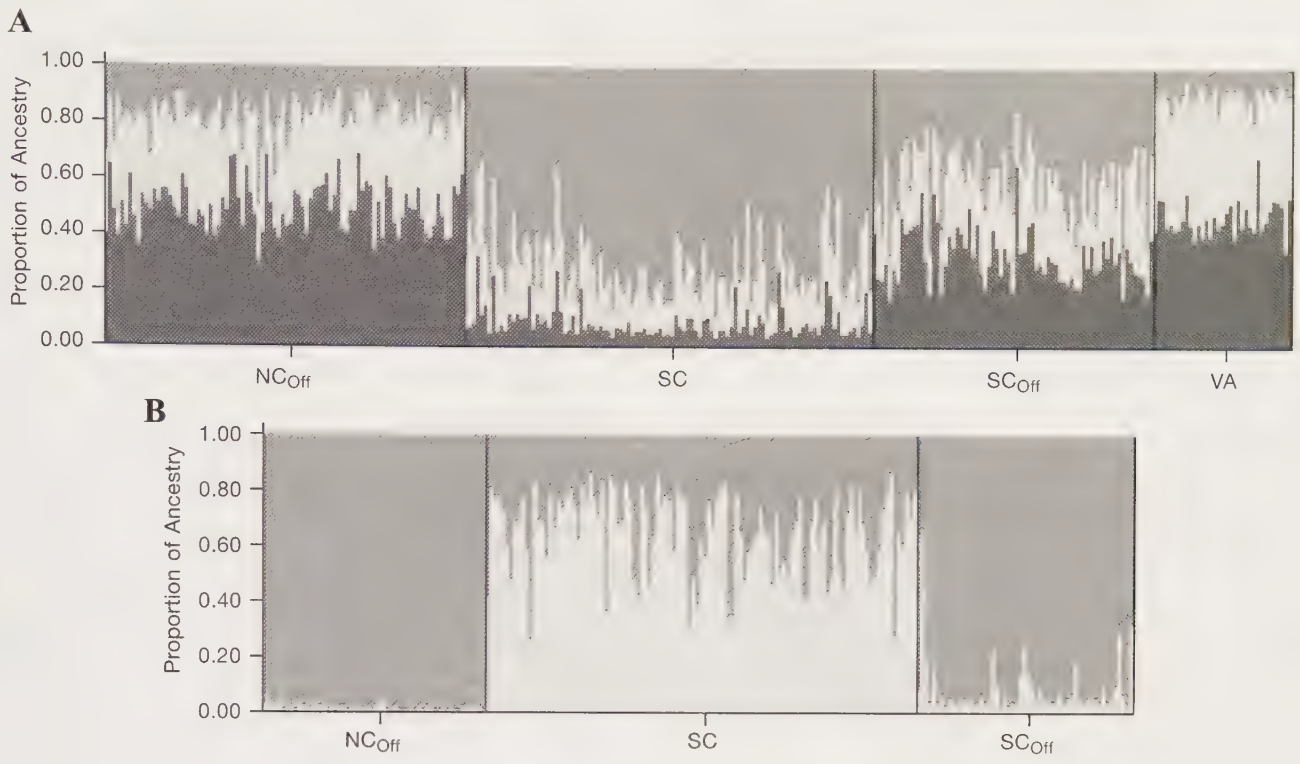

Figure 2

Results of genetic analyses with the use of Structure software for (**A**) the 2008 and (**B**) 2009 collections of Cobia (*Rachycentron canadum*), where each column represents an individual sample and the shades of gray represent the ancestral populations. Multiple shades within a column indicate an individual of mixed ancestry. Collection locations are grouped together and are the following: offshore North Carolina (NC_{Off}), inshore South Carolina (SC), offshore South Carolina (SC_{Off}), and inshore Virginia (VA).

The genesis of Cobia research in SC began with the need to collect life history information to explore the potential of this species for aquaculture production and to better understand the impact stocking may have on a highly migratory species. The scope of our program not only encompassed gathering information on basic life history and population dynamics from the wild population, but also incorporated information on tagged stocked animals to better understand movement patterns and fidelity to natal estuaries. Collection of such information has proven to be useful for interpreting genetic results. The detection of stocked fish from multiple year classes of fish released within the Port Royal Sound estuary was somewhat unexpected given the many unknowns regarding Cobia life history (e.g., their use of juvenile habitat, their home ranges, movement patterns, and spawning migrations). Although the initial 1.1% contribution to the 2004 YC appears low, when considering the limited number of fish originally released, we interpreted these results as being pos-

Table 9

Summary of genetic diversity statistics pooled across collection years for Cobia (*Rachycentron canadum*). Collection locations included inshore Virginia (VA), offshore North Carolina (NC_{Off}), inshore South Carolina (SC), and offshore South Carolina (SC_{Off}). n=sample size, N_A=average number of alleles per locus, H_O=average observed heterozygosity across loci, H_E=average expected heterozygosity across loci, F_{IS}=inbreeding coefficient.

Collection location	n	N_A	H_O	H_E	F_{IS}
VA	35	10.4	0.772	0.768	0.07
NC_{Off}	146	14.0	0.762	0.757	–0.01
SC	212	11.5	0.709	0.717	–0.03
SC_{Off}	126	12.7	0.745	0.753	–0.05

itive in terms of the potential for stock enhancement to be effective as a fisheries management tool for Cobia. The results show how understanding life history attributes is necessary to designing a stocking program for a highly migratory pelagic species. The much higher stocking contribution observed in 2009 following the larger 2007 YC release during their first year of potential recruitment to the fishing gear provides additional support for the efficacy of stock enhancement. Furthermore, the recapture of these stocked fish within their release estuary two years after release indicates that some degree of estuarine fidelity occurs within these inshore Cobia aggregations, supporting the identification of the unique genetic structure in wild fish populations. Estuarine fidelity is also indicated by the recapture of an individual wild fish within the Port Royal Sound estuary during multiple collection years; as well as by the high incidence of external tag recapture reports occurring within the Port Royal Sound area. Therefore, these results complement both the previously observed high site fidelity in SC (Hammond[3]) and Lefebvre and Denson's (2012) documented spawning function of the inshore aggregations on the basis of positive Cobia egg and larval detection within the Port Royal Sound estuary.

In the Persian Gulf and Oman Sea, Salari Aliabadi et al. (2008) also investigated small-scale population structure in Cobias, using microsatellite markers. Although they reported the presence of 3 distinct genetic populations along their northern coasts, their study was likely confounded by small sample sizes, lack of a temporal sampling design, and no corrections for multiple comparisons in their analyses as they were unable to identify any potential behavioral or geographic mechanisms of genetic isolation among detected groupings. In contrast, we used robust sampling and analysis approaches that provided links between the detected genetic structure and the several indications of mechanisms of genetic isolation (seasonal aggregations and estuarine fidelity).

Conclusions

The genetic diversity, in terms of both gene diversity and allelic richness, detected in Cobias along the southeastern U.S. Atlantic coast is similar to that reported in both Iran (Salari Aliabadi et al., 2008) and the northern Gulf of Mexico (Pruett et al., 2005), and all metrics are somewhat higher than the averages reported for marine fishes (DeWoody and Avise, 2000). Therefore, on the basis of the genetic characterization along the southeastern Atlantic coast of the United States, Cobia appears to be quite genetically diverse both overall and within localized areas and exhibits temporal stability over the project period. However, the detection of discrete genetic structure for Cobia within this portion of its range has implications for the appropriate management of this important recreational fisheries species.

As with many aspects of Cobia's life history, the implications of our genetic results for management are not straightforward. For example, information gathered from the offshore collections shows high levels of movement along the southeastern U.S. Atlantic, and a recommendation founded only on that observation might include continuation of the single population management strategy because overfishing in one offshore area would affect other areas as well. In contrast, a recommendation made solely on the basis of the inshore collections that indicate the presence of distinct population segments and estuarine fidelity in Cobia might favor separate management of the population segments because localized fishing pressure would primarily impact the local population. However, perhaps given the complicated life history of the Cobia, a more appropriate recommendation would be to use a 2-tiered strategy, in which Cobias are managed regionally as a single population for offshore fishery activities, but are also managed at the local level (state management) for aggregation-specific inshore fishing activities. Considering the genetic uniqueness of the inshore aggregations, there is concern that the majority of the fishing pressure on these aggregations targets the reproductive pool of Cobia on their spawning grounds. Although there is still much to learn about the intricacies of Cobia life history, the results presented here are needed for informed decisions regarding the future management of this recreationally and commercially important species.

Acknowledgments

The authors wish to thank the charter boat captains and cooperating fishermen in VA, NC, SC, and Florida who provided genetic samples and reported external tags—for their efforts without which we would not have been able to complete this research. We also thank L. Borecki, B. Cushman, D. Farrae, M. Jamison, W. Jenkins, L. Lefebvre, B. McAbee, M. Perkinson, and C. Tarpey for providing invaluable assistance and comments on this project. We appreciate the cooperation of M. Renshaw and J. Gold during our initial project work. Our work was funded in part by the South Carolina Department of Natural Resources and grant no. 114775-GL10013 (grant in aid no. NA16RG1646) from the National Marine Aquaculture Initiative of the National Oceanic and Atmospheric Administration. This publication is number 692 from the Marine Resources Research Institute.

[3] Hammond, D. 2001. Status of the South Carolina fishery for cobia. South Carolina Department of Natural Resources Technical Report Number 89, 22 p. [Available from the Office of Fisheries Management, Marine Resources Division, South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, SC 29422-2559.]

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Co-occurrence of bycatch and target species in the groundfish demersal trawl fishery of the U.S. west coast; with special consideration of rebuilding stocks

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Abstract—Bycatch and resultant discard mortality are issues of global concern. The groundfish demersal trawl fishery on the west coast of the United States is a multispecies fishery with significant catch of target and nontarget species. These catches are of particular concern in regard to species that have previously been declared overfished and are currently rebuilding biomass back to target levels. To understand these interactions better, we used data from the West Coast Groundfish Observer Program in a series of cluster analyses to evaluate 3 questions: 1) Are there identifiable associations between species caught in the bottom trawl fishery; 2) Do species that are undergoing population rebuilding toward target biomass levels ("rebuilding species") cluster with targeted species in a consistent way; 3) Are the relationships between rebuilding bycatch species and target species more resolved at particular spatial scales or are relationships spatially consistent across the whole data set? Two strong species clusters emerged—a deepwater slope cluster and a shelf cluster—neither of which included rebuilding species. The likelihood of encountering rebuilding rockfish species is relatively low. To evaluate whether weak clustering of rebuilding rockfish was attributable to their low rate of occurrence, we specified null models of species occurrence. Results indicated that the ability to predict occurrence of rebuilding rockfish when target species were caught was low. Cluster analyses performed at a variety of spatial scales indicated that the most reliable clustering of rebuilding species was at the spatial scale of individual fishing ports. This finding underscores the value of spatially resolved data for fishery management.

Manuscript submitted 19 January 2013.
Manuscript accepted 25 November 2013.
Fish. Bull. 112:36–48 (2014).
doi: 10.7755/FB.112.1.3

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Bycatch, catch of incidental (nontarget) species, is a major source of fish removals, and thus is a concern in fisheries around the world. Its impact on biodiversity and habitat health may be extensive (Dayton et al., 1995; Collie et al., 1997; Jennings and Kaiser, 1998; Thrush and Dayton, 2002), and, consequently, it has the potential to affect the long-term sustainability of marine fisheries and ecosystems. Several articles have emphasized the need for ecosystem management to address the population health of both targeted and nontarget species (Pauly et al., 2000; Pikitch et al., 2004; Beddington et al. 2007). A comprehensive understanding of the species composition and characteristics of bycatch could contribute to a greater knowledge of the effects of marine fisheries on ecosystems (Goni, 1998).

Bycatch is particularly pertinent for multispecies fisheries, where the gear often cannot fully separate targeted and nontarget species. The groundfish fishery on the west coast of the United States (Fig. 1) is a multispecies fishery that primarily targets demersal fish species such as Sablefish (*Anoplopoma fimbria*), Dover Sole (*Microstomus pacificus*), Shortspine Thornyhead (*Sebastolobus alascanus*), Petrale Sole (*Eopsetta jordani*), and Pacific Hake (*Merluccius productus*). The majority of catch is acquired through the use of bottom-trawl nets, which are considered one of the least discriminating gear types (Alverson et al., 1994). The depths at which fish are caught and from which fish are raised to the ocean surface also cause mortality. Despite the long history of bottom-trawl fishing on the west coast of the United States, information on the species composition of bycatch in this fishery has only recently been regularly collected (Bellman and Heery, 2013).

A clear understanding of species co-occurrence in the total catch is important for anticipating the ecological impacts of bycatch. Since 2002, bycatch data have been collected in the bottom trawl (non-hake) fishery by at-sea observers and are used by fishery managers in a variety of ways. Perhaps the most important

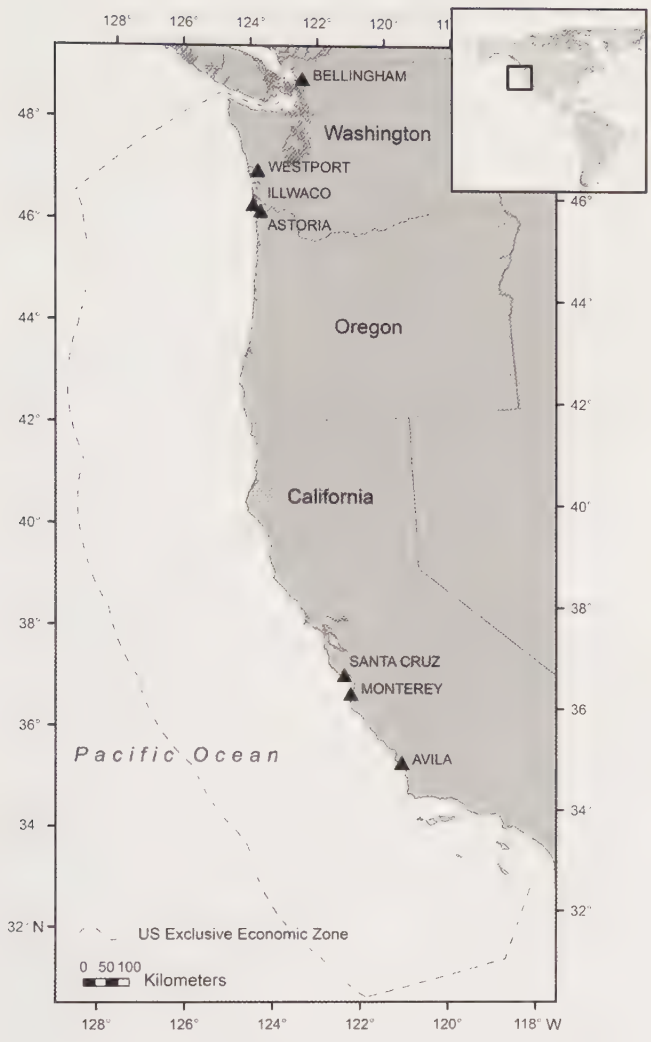

Figure 1

Map of the study area from northern Washington to southern California where catch data were collected by observers from 2002 to 2009. In cluster analyses, clusters containing rebuilding species were most evident when the data for each port were evaluated separately. The map highlights examples of port groups in which relationships between rare rebuilding rockfish and target species were identified in the commercial catch. Courtesy of M. Bellman.

role of observer data for management is for the calculation of bycatch ratios. Bycatch ratios reflect the amount of catch of incidental (nontarget) species that occurs in relation to the amount of retained catch of species that are targeted by the fishery. Managers produce projected estimates of bycatch for nontarget species on the basis of such ratios in conjunction with anticipated landings (Bellman and Heery, 2013). This approach assumes that there is a proportional relationship between bycatch and landings of target species (Rochet and Trenkel, 2005).

Several previous studies have examined assemblages among groundfish species through the use of data from fishery-independent surveys (Gabriel and Tyler, 1980; Weinberg, 1994; Jay, 1996; Williams and Ralston, 2002; Tolimieri and Levin, 2006; Zimmerman, 2006; Cope and Haltuch, 2012). There have been fewer studies of species associations with the use of fishery-dependent data. Lee and Sampson (2000) used logbook data to evaluate species composition in the bottom trawl fishery. Trawl logbooks are maintained by vessel captains and include only species that are retained and landed. Their study, therefore, did not include species that were also caught by trawl nets but that were discarded because of economic or regulatory constraints. Rogers and Pikitch (1992) used observer data to identify species assemblages, but participation in the observer program that produced their data was voluntary. The data available for that study were collected between 1985 and 1987, a period in which fishery practices and regulations differed considerably from those used more recently.

This study presents a current view of species co-occurrence onboard commercial vessels in the bottom trawl fishery, and with the use of data from a mandatory at-sea observer program conducted yearly from 2002 to 2009, is more comprehensive than that of previous studies. Three major questions were explored: 1) Are there identifiable associations between species caught in the bottom trawl fishery? 2) Do species that are undergoing population rebuilding toward target biomass levels ("rebuilding species") cluster with targeted species in a consistent way? 3) Are the relationships between rebuilding species and target species more resolved at particular spatial scales or are relationships spatially consistent across the whole data set? All groundfish species that were managed under federal rebuilding plans during the study period were considered as rebuilding species. The results from our analysis relate indirectly to species assemblages in the marine environment. However, the study is primarily relevant in the context of fisheries management because it provides insight into the relationship between bycatch of nontarget species and catch of targeted species in the commercial catch of the demersal trawl fishery on the west coast of the United States.

Materials and methods

At-sea observer data

Observer data were obtained from the West Coast Groundfish Observer Program (WCGOP), part of the National Marine Fisheries Service (NMFS). The WCGOP employs a stratified multistage random sampling design in which permits for the coastwide limited entry trawl fishery are selected for 2-month periods without replacement until all permits in the fleet are observed. The vast majority of permits were linked to individual

vessels during the study period. Information on switching of permits between vessels could not be disclosed for the few instances when it occurred, for reasons of confidentiality, but the distinction between permits and vessels is not important for our study. Data were collected on all trips and tows within the 2-month period for which a permit was selected. The data used for this analysis were collected from January 2002 through December 2009. During this period, the observer program cycled through all nonexempt permits (exemptions were given because of safety concerns) in the limited entry bottom trawl fleet 10 times.

While onboard, observers quantified the total discard weight of each species on each tow and collected biological samples from discards through subsampling procedures that are documented elsewhere (NWFSC[1]). Observers focused their attention foremost on discarded catch because data on discards could not be obtained from other sources, unlike landed catch for which data were available from vessel logbooks and landing receipts. Retained catch weights were acquired from the vessel logbook or by visual estimation of the proportion of the codend or trawl alley (the area where the trawl is placed after retrieval) that was filled. These estimates were then reconciled with weights from landing receipts for each observed trip. Through this process of reconciling the 2 data sources, changes were made to the retained weights on 94% of observed trips. When landings records were not available for an observed trip, retained weights originally recorded by the observer were used. Further information regarding the sampling scheme and data quality control process are available online at http://www.nwfsc.noaa.gov/research/divisions/fram/observer/.

To begin our analysis, presence and absence information for each tow was compiled from the observer data set. Although abundance data would give information on the magnitude of bycatch, the use of abundance data for our analysis would yield associations primarily between species that co-occur at similar catch levels. Although interesting for other research questions, those abundance-dominated associations were not informative for our analysis of co-occurrence of rebuilding bycatch species and target species. Additional available fields that were used in the analysis included average latitude, longitude, average depth, departure and return ports, and tow duration, among others. The data contained catch information for 175 different species from 45,252 tows. All groundfish species that occurred in at least 5% of tows or more were included, eliminating 138 species from the analysis that were not the target and rebuilding bycatch species of interest for our study. In addition, 7 species designated as "overfished" by NMFS were considered in the analysis. Under federal law, a rebuilding plan must be developed for any fish species that is designated as "overfished" in relation to limit reference points (standardized thresholds used to determine stock status) (Restrepo et al., 1998). These species included Bocaccio (*Sebastes paucispinis*), Canary Rockfish (*S. pinniger*), Cowcod (*S. levis*), Darkblotched Rockfish (*S. crameri*), Pacific Ocean Perch (*S. alutus*), Widow Rockfish (*S. entomelas*), and Yelloweye Rockfish (*S. ruberrimus*).

[1] NWFSC (Northwest Fisheries Science Center). 2007. West coast groundfish observer training manual. [Available from NWFSC West Coast Groundfish Observer Program, 2725 Montlake Blvd. East, Seattle, WA 98112.]

Cluster analysis

Cluster analyses are commonly used to identify fish species assemblages (Williams and Ralston, 2002). Many approaches to clustering analysis exist and resultant groupings are always relative to the units being grouped and the algorithm used to process the distance matrix (Gordon, 1999). Multiple methods of clustering the data were used to make results and conclusions more robust (Mahon et al., 1998). We focused on 2 main approaches: 1) Hierarchical agglomerative cluster analysis (HCA) and 2) Nonhierarchical cluster analysis, or partitioning analysis (PA) (Cope and Haltuch, 2012).

With the HCA approach, all elements are assumed to be a separate cluster and groups are established by subsequently merging elements to maximize the average distances between all elements within each cluster. Partitioning analysis, with the k-medoids approach, requires specifying beforehand the number of desired clusters from which the grouping algorithm minimizes dissimilarity between elements within clusters (Cope and Punt, 2009). Partitioning analysis thus requires the additional step of identifying the optimal number of clusters (k) supported by the data. This step is accomplished by using cluster validity diagnostics. After considering several of them through simulation, Cope and Punt (2009) found 2 cluster validity diagnostics that performed best: average silhouette coefficient (Kauffman and Rousseeuw, 2005) and Hubert's Γ (Gordon, 1999). Because these diagnostics have a tendency to either overlump or oversplit groups, respectively, both of them were used to identify the optimal number of clusters. In instances where the 2 diagnostics supported different numbers of optimal clusters, both sets of clusters were retained for evaluation. The Bray-Curtis dissimilarity measure was used to transform species presence and absence information by tow into a dissimilarity matrix used by both clustering approaches.

Once species were clustered, the next task was to identify which of the clusters were dissimilar enough from others to be considered distinct. Guidance for interpreting the clusters in a PA was provided in Kauffman and Rousseeuw (2005), who identified an average group silhouette value >0.25 as being sufficiently distinct from other groups. For the HCA, it was less clear what constituted a group. We followed the approach of Cope and Haltuch (2012) who introduced a null model approach to define significant groups when using HCA.

This approach added "fake" species (termed "fakies") to the data set that were randomly allocated to each tow (i.e., a 0.5 probability of occurring in any tow) and were subsequently clustered as members of the full data set. The dissimilarity point at which these species were grouped (termed the "breakpoint") represented the dissimilarity distance at which group assignments were considered to be no better than random placement. This breakpoint was not affected by the number of fakies included in the analyses (Cope and Haltuch, 2012). Here the results are presented for cases where 5 fakies were added.

Results from the HCA and the PA (with the use of both the silhouette coefficient and Hubert's Γ cluster validity diagnostics) were then compared and reconciled. Reconciliation was performed by looking for consistently forming groups of co-occurring species in the catch that were supported by all clustering methods. Instances of groups being supported by 1, but not both, cluster approaches were noted. Throughout the presentation of our results, we use the term "identifiable" clusters to represent clustered species that 1) had an average silhouette value >0.25 in each PA (Kauffman and Rousseeuw, 2005) and 2) a dissimilarity point that was less than that for simulated fake species in HCA results (Cope and Haltuch, 2012).

Species assemblage analyses were completed on various subsets of the data to evaluate species co-occurrence in the demersal trawl fishery at a variety of temporal and spatial scales. These analyses helped to resolve fine-scale aspects of species co-occurrence with rebuilding species in the commercial catch. Assemblages were first evaluated on a coastwide basis by applying each clustering method to the data as a whole. The next part of the analyses partitioned the data by year. Additionally, dominant clusters sometimes obscured smaller, but nonetheless identifiable groupings. To avoid such an outcome, we removed the ubiquitous species that had formed clusters when using all species combined and then ran all cluster analyses again with the remaining species to identify additional assemblages.

Rebuilding species

The characterization of species assemblages containing rebuilding species was an important consideration, yet the rebuilding species were some of the rarest of the species included in our data set. Thus, it was unlikely that they would be well represented in any assemblage. Three approaches were taken to resolve the co-occurring relationship of rebuilding species with other species in the commercial catch data. With the first approach, we compared the proximity of rebuilding species with that of the simulated fakies that occurred with decreasing frequency. Cluster analyses were explored with the occurrence probability of fakies on each tow (x) set equal to the frequency of occurrence of each rebuilding species (Table 1). This exploration allowed evaluation of the level of random assignment which best described the presence of rebuilding species in clusters. For example, if a species had a 5% frequency of occurrence, a probability of assigning a fakie to a tow was also set at 5%. A dissimilarity distance equal to or greater than the breakpoint of the fakies would indicate a randomly occurring, and therefore not a co-occurring, rebuilding species.

With the second approach, we considered species co-occurrences only in the rare occasions when a rebuilding species was present on a tow, thus defining species assemblages as conditional on the presence of a rebuilding species. Using only positive tows for each rebuilding species as data sets, we re-analyzed clusters, and species assemblages were identified on a coastwide, year-by-year basis. Fakies were also incorporated into this analysis to define clusters.

With the third approach, we evaluated species assemblages at finer spatial resolutions to identify spatially explicit co-occurrences with rebuilding species in the catch. For each rebuilding species, a tree regression was applied to identify a spatial stratification scheme on the basis of latitude. Tree regression uses recursive partitioning to split data into groups (Clark and Pregibon, 1992). In this case, the data were split by latitude on the basis of the log-transformed catch per tow of each rebuilding species and thus identified hot spots of species catch. Cluster analysis was then applied within each of the resulting latitudinal strata. Additionally, data were stratified with 1° latitude intervals, as well as on the basis of the departure port recorded by the observer. Clustering results from these 3 stratification schemes were then compared and summarized.

All analyses described here were conducted in R software (vers. 2.13.2; R Development Core Team, 2011[2]).

Results

Overall species co-occurrences

When using observer data from all areas and all years, we found 2 strong and consistent clusters: 1) a deepwater slope cluster and 2) a shelf cluster (Table 2, Fig. 2). The most common components of the slope cluster were Sablefish, Dover Sole, and Shortspine Thornyhead. This group also included Arrowtooth Flounder (*Atheresthes stomias*), Rex Sole (*Glyptocephalus zachirus*), Longnose Skate (*Raja rhina*), and Pacific Hake, depending on the method used to determine clusters. The major constituents of the shelf cluster were English Sole (*Parophrys vetulus*) and Petrale Sole. Hierarchical clustering analysis also indicated that Lingcod (*Ophiodon elongatus*), Pacific Spiny Dogfish (*Squalus suckleyi*), and Spotted Ratfish (*Hydrolagus colliei*) were

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Groundfish species that were included in cluster analyses and the percentage of "inshore" and "offshore" tows during which they were observed for the period of 2002–09 in the groundfish fishery of the U.S. west coast. Inshore was defined as all tows occurring at an average depth of 274 m (150 fathoms) or less. Offshore tows were those for which the average depth was greater than 150 fathoms. Rebuilding rockfish species and their respective percentages on inshore and offshore tows are underlined. Major target species are noted by an asterisk.

Common name	Scientific name	% of inshore tows	% of offshore tows
Arrowtooth Flounder*	*Atheresthes stomias*	64.5	55.7
Aurora Rockfish	*Sebastes aurora*	0.7	25.9
Big Skate	*Raja binoculata*	26.8	1.3
Bocaccio	*Sebastes paucispinis*	5.3	0.9
Canary Rockfish	*Sebastes pinniger*	18.2	0.6
Cowcod	*Sebastes levis*	1.3	0.1
Darkblotched Rockfish	*Sebastes crameri*	15.7	18.2
Dover Sole*	*Microstomus pacificus*	75.1	93.0
English Sole*	*Parophrys vetulus*	80.7	10.5
Flathead Sole	*Hippoglossoides elassodon*	20.5	0.1
Greenstriped Rockfish	*Sebastes elongatus*	28.4	1.3
Grenadiers	Macrouridae	0.4	12.8
Lingcod	*Ophiodon elongatus*	65.2	9.4
Longnose Skate*	*Raja rhina*	48.3	48.3
Longspine Thornyhead*	*Sebastolobus altivelis*	0.3	60.9
Mixed Thornyheads*	*Sebastolobus* spp.	0.3	13.0
Other rockfish	*Sebastes* spp.	6.9	28.0
Other sanddabs	*Citharichthys* spp.	33.4	0.1
Other skates	Rajiformes	61.4	40.0
Pacific Cod	*Gadus macrocephalus*	28.2	1.0
Pacific Flatnose	*Antimora micolepis*	0.0	21.3
Pacific Grenadier	*Coryphaenoides acrolepis*	0.0	22.6
Pacific Hake	*Merluccius productus*	56.0	70.9
Pacific Halibut	*Hippoglossus stenolepis*	44.8	22.6
Pacific Ocean Perch	*Sebastes alutus*	2.5	15.8
Pacific Sanddab	*Citharichthys sordidus*	48.7	0.5
Petrale Sole*	*Eopsetta jordani*	85.7	22.4
Redbanded Rockfish	*Sebastes babcocki*	2.5	13.0
Rex Sole*	*Glyptocephalus zachirus*	81.6	47.7
Rosethorn Rockfish	*Sebastes helvomaculatus*	2.3	9.0
Sablefish*	*Anoplopoma fimbria*	50.0	95.2
Shortspine Thornyhead*	*Sebastolobus alascanus*	5.4	87.8
Pacific Spiny Dogfish	*Squalus suckleyi*	57.7	33.9
Splitnose Rockfish	*Sebastes diploproa*	4.4	30.5
Spotted Ratfish	*Hydrolagus colliei*	70.9	30.0
Widow Rockfish	*Sebastes entomelas*	1.9	1.6
Yelloweye Rockfish	*Sebastes ruberrimus*	1.3	0.1

part of the shelf cluster, but this result was not confirmed by partitioning analysis. These groups were consistent with those found by Cope and Haltuch (2012), who used fishery-independent data. Species were identified as slope or shelf species on the basis of their depth distribution in the groundfish bottom trawl survey (Keller et al., 2012).

All of the species shown to cluster in this first round of analysis were relatively common, occurring on at least 35% of tows (Table 1). These species were the only ones to form clusters more readily than fakies, which were grouped at a silhouette value just above 0.25 in each PA (consistent with the recommendation of Kauffman and Rousseeuw [2005]) and at a distance of approximately 0.4 in the HCA (consistent with Weinberg [1994]). Rebuilding and less common species were not components of clusters at a coastwide level and clustered less readily than fakies, which had been simulated to occur at random.

Similar trends were observed when the data were broken out by year. Only the most common species formed clusters more readily than fakies on an annual,

Table 2

Results from hierarchical agglomerative cluster analyses (HCAs) of groundfish species and simulated, random fake species ("fakies"). Only species that formed groups more readily than fakies are included. Species that exhibited the strongest association with other species in their respective group are set in italic type. Groups A, C, and D included species commonly associated with the continental slope, and group B included species associated with shelf habitats. Note that the "skates" category included Longnose Skate from 2002 to 2004, causing it to cluster with slope species. Longnose Skate were recorded under a distinct species code starting in 2005.

Species	2002	2003	2004	2005	2006	2007	2008	2009
Dover Sole	A	A	A	A	A	A	A	A
Sablefish	A	A	A	A	A	A	A	A
Pacific Hake	A	A	A	A	A	A	A	A
Arrowtooth Flounder	A	A	A	A	A	A	A	A
Skates	A	A	A					
Longnose Skate				A	A	A	A	A
Rex Sole	A	A	A	B	B	A		
Petrale Sole	B	B	B	B	B	B	B	B
English Sole	B	B	B	B	B	B	B	B
Lingcod	B	B	B	B	B	B		B
Spotted Ratfish	B	B	B	B	B	B		
Pacific Sanddab	B							B
Pacific Spiny Dogfish				B	B	B		
Longspine Thornyhead	C	A	C	C	C		A	A
Shortspine Thornyhead	C	A	C	C	C	A	A	A
Pacific Flatnose					D			
Pacific Grenadier					D			

coastwide basis. The 2 major clusters identified in the run with combined areas over all years were generally recognized annually as well (Table 2). Dover Sole, Sablefish, Pacific Hake, and Arrowtooth Flounder consistently clustered together in all years. Skates were also grouped with these species in 2002 through 2004. From 2005 through 2009, Longnose Skate was instead clustered with the Dover Sole+Sablefish group. This occurrence is likely due to a shift in the way skate species were recorded in the observer data. Before 2005, Longnose Skate were given the species code for the unspecified skate category.

Shortspine Thornyhead and Longspine Thornyead were only part of the cluster of slope species in some years during the time series (Table 2). In 2002, 2004, 2005, and 2006, they formed a cluster with each other and with no other species. Petrale Sole and English Sole formed a consistent group in all years. Depending on the year, they were also grouped with Lingcod, Spotted Ratfish, Rex Sole, Pacific Spiny Dogfish, and Pacific Sanddab (*Citharichthys sordidus*) (Table 2).

When ubiquitous species that formed an identifiable assemblage on a coastwide basis were removed from the data and the analysis of all years of data was rerun, no further groupings were identified to cluster more readily than were the fakies. The same was true when identified assemblages were removed from the data and analyses were conducted separately for each year.

Rebuilding bycatch species

We used 2 data treatments to discern co-occurrences of rebuilding species with other species in trawl catch. In the first treatment, simulated fakies were introduced at frequencies of occurrence that matched those of the respective rebuilding species. This step was taken to evaluate whether the rebuilding species grouped in a better-than-expected manner on the basis of frequency of occurrence alone. Bocaccio, Cowcod, Canary Rockfish, Darkblotched Rockfish, Pacific Ocean Perch, and Widow Rockfish all formed groups with target species more readily than did fakies that were simulated on the basis of the percent occurrence of each rebuilding species. This observation indicates the tendency for rebuilding species to cluster more than expected from their low encounter rates. Yelloweye Rockfish, which occurred in 0.6% of tows, was the only rebuilding rockfish species that did not form groups more than the simulated fakies.

With the second treatment, we evaluated whether rebuilding species formed clusters with any other species, using only the positive occurrence data for the rebuilding species in question (i.e., only tows where that rebuilding species was encountered). An example for Canary Rockfish is presented in Figure 3. In all cases, this step resulted in one large cluster that inevitably contained the rebuilding species in question, along with those species that occur most commonly in the bottom

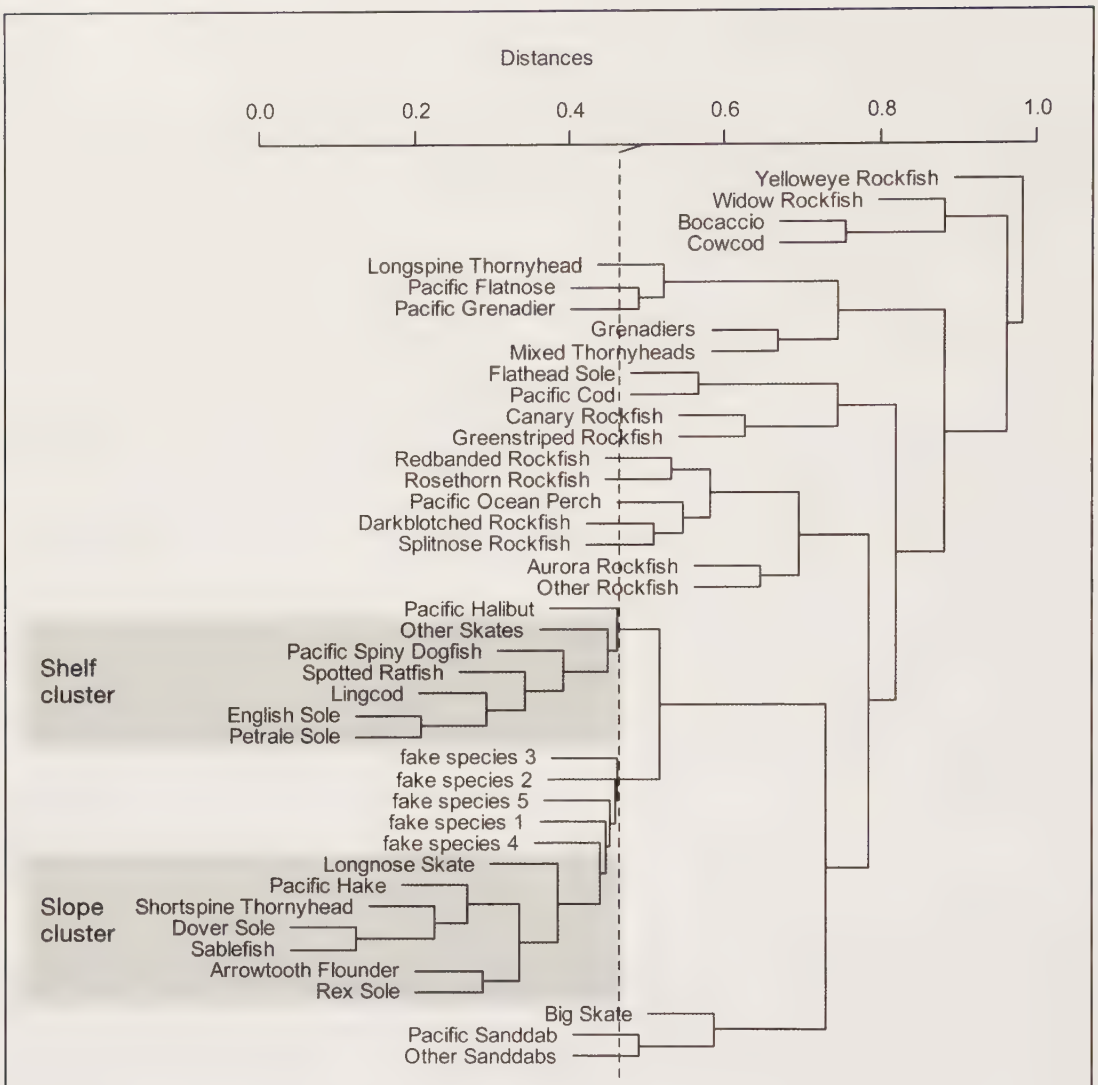

Figure 2

Dendrogram of species clusters determined with hierarchical cluster analysis for the entire geographic range of the demersal trawl fishery for all years (2002–09). Fake, simulated species ("fakies") were included in the analysis as a means of identifying the dissimilarity distance for identifiable clusters. A dashed line shows the dissimilarity distance attributed to fakies (i.e., the breakpoint less than which clusters are considered to be identifiable). The distance axis represents dissimilarity measures determined from the cluster analysis. Two clusters are evident, a slope cluster consisting of demersal species associated with the continental slope, and a shelf cluster consisting of species commonly associated with the continental shelf. Groupings that included rebuilding species all had dissimilarity distances that were greater than randomly simulated "fakies."

trawl fishery. Rebuilding species that are associated with continental shelf habitats (Canary Rockfish, Yelloweye Rockfish, and Bocaccio) did tend to cluster more closely with shelf target species such as English Sole, Petrale Sole, and Lingcod. However, they were all still part of a larger cluster that also included Sablefish, Dover Sole, and other slope species. These large clusters had a silhouette value <0.25 (for PA analyses) and a distance measure less than 0.4 (for HCA), both indicating insignificant groupings. Rebuilding species were grouped with the most common species by default. When a rebuilding species was caught, a series of other commonly occurring target species were likely to have been caught as well, but the opposite could not be stated. As an example, a tow in which Canary Rockfish was caught was also likely to have caught Petrale

Table 3

Results from tree regressions for 5 rare rebuilding rockfish species. Tree regressions were conducted for each rebuilding species that did not form identifiable clusters in initial cluster analyses in which all species were included and were used to develop strata boundaries for additional cluster analyses. A minimum sample size of 100 tows was required within each stratum. Strata selected from the tree regression produced the same clustering results that were observed when data from the entire coast were analyzed: No clusters containing rebuilding species were evident.

Species	Stratification
Bocaccio	46°39.62′, 39°53.32′, and 38°47.20′N latitude
Canary Rockfish	47°13.70′, 46°10.72′, and 45°13.19′N latitude
Cowcod	No suitable strata
Widow Rockfish	46°05.49′ and 40°32.46′N latitude
Yelloweye Rockfish	47°43.28′ and 46°13.53′N latitude

Sole, English Sole, and Lingcod, but catch of these 3 species did not serve as an indicator for the potential of encountering Canary Rockfish (Fig. 3).

Next we evaluated whether rebuilding species were part of recognizable species assemblages at a finer spatial resolution. This step was undertaken by conducting 3 sets of cluster analyses that had been stratified 1) by using tree regression, 2) by using 1° latitudinal strata, and 3) by departure port. Results from the tree regression used to divide tows into latitudinal strata are shown in Table 3. Strata selected from the tree regression produced the same clustering results that were observed when data from the entire coast were analyzed: no clusters containing rebuilding species were evident. The large size of latitudinal strata identified by tree regression may explain the similarity of these results to the coastwide data results.

To evaluate species assemblages on an even finer scale, the data were divided into smaller latitudinal strata (1° intervals). At this spatial resolution rebuilding bycatch species formed clusters in 1 area, between 35° and 36° north latitude, where Bocaccio was grouped with English Sole (Table 4). PA results indicated that the Widow Rockfish was also a part of this assemblage, but this finding was not confirmed by HCA. This area contained a relatively small number of observations with a total of 367 observed tows across all years. In other areas, there did appear to be a loose relationship between Canary Rockfish and Greenstriped Rockfish (*Sebastes elongatus*). However, this result was not confirmed by all clustering methods and, therefore, was not recognized as a meaningful result, particularly given that Greenstriped Rockfish is not a targeted species.

Clusters containing rebuilding species were more evident when the data were stratified by departure port. Table 5 details the results of cluster analysis for each port group separately. Rebuilding species formed clusters in several southern port groups. However, the sample size for these ports was also relatively small. For instance, Bocaccio grouped with several slope species, including Sablefish, Dover Sole, and Pacific Hake, when caught by 6 different vessels originating in Santa Cruz and Monterey. All together, these vessels made a total of 294 observed tows (out of 27,162 total tows coastwide) from 2002 through 2009. Additionally, Cowcod was associated with Pacific Sanddab (*Citharichthys sordidus*) in the catch of observed vessels from Avila. These vessels, 7 in total, made 108 observed tows throughout the entire time series.

Farther to the north, vessels departing from Astoria, Westport, and Ilwaco (Fig. 1) tended to catch Pacific Ocean Perch with 2 nonrebuilding slope rockfish species: Redbanded Rockfish (*Sebastes babcocki*) and Splitnose Rockfish (*S. diploproa*). This slope rockfish cluster was distinct from the slope species assemblage of Sablefish, Dover Sole, and others (Table 5). For Bellingham vessels, the slope rockfish assemblage also included Darkblotched Rockfish.

Discussion

In this analysis, we sought to identify whether there were consistently observed associations between target and nontarget species in commercial catches monitored by fisheries observers, who are the source of data usually available to fishery managers for bycatch, or whether the species composition in the commercial catch might be better described as random. We placed particular emphasis on the bycatch of rare, but important rebuilding species. Such bycatch of rebuilding species can delay recovery of overfished stocks and limit target fisheries. When evaluating data from the entire geographic range of the fishery, we found 2 distinct species assemblages that consistently grouped more readily than did randomly simulated fakies: a deepwater slope group characterized by Dover Sole and Sablefish and a shallower shelf group dominated by English Sole and Petrale Sole (Fig. 2).

Distinct groups of deepwater slope and shelf species have been a consistent finding in studies of species assemblages among west coast groundfish (Gabriel and Tyler, 1980; Rogers and Pikitch, 1992; Jay, 1996; Lee and Sampson, 2000; Tolimieri and Levin, 2006; Zimmerman, 2006; Cope and Haltuch, 2012). The study of Rogers and Pikitch (1992) is perhaps the most similar to our study, because of their use of observer data and similar quantitative methods. The shelf assemblage identified by Rogers and Pikitch (1992) included sanddabs, English Sole, Sand Sole (*Psettichthys melanostictus*), Starry Flounder (*Platichthys stellatus*),

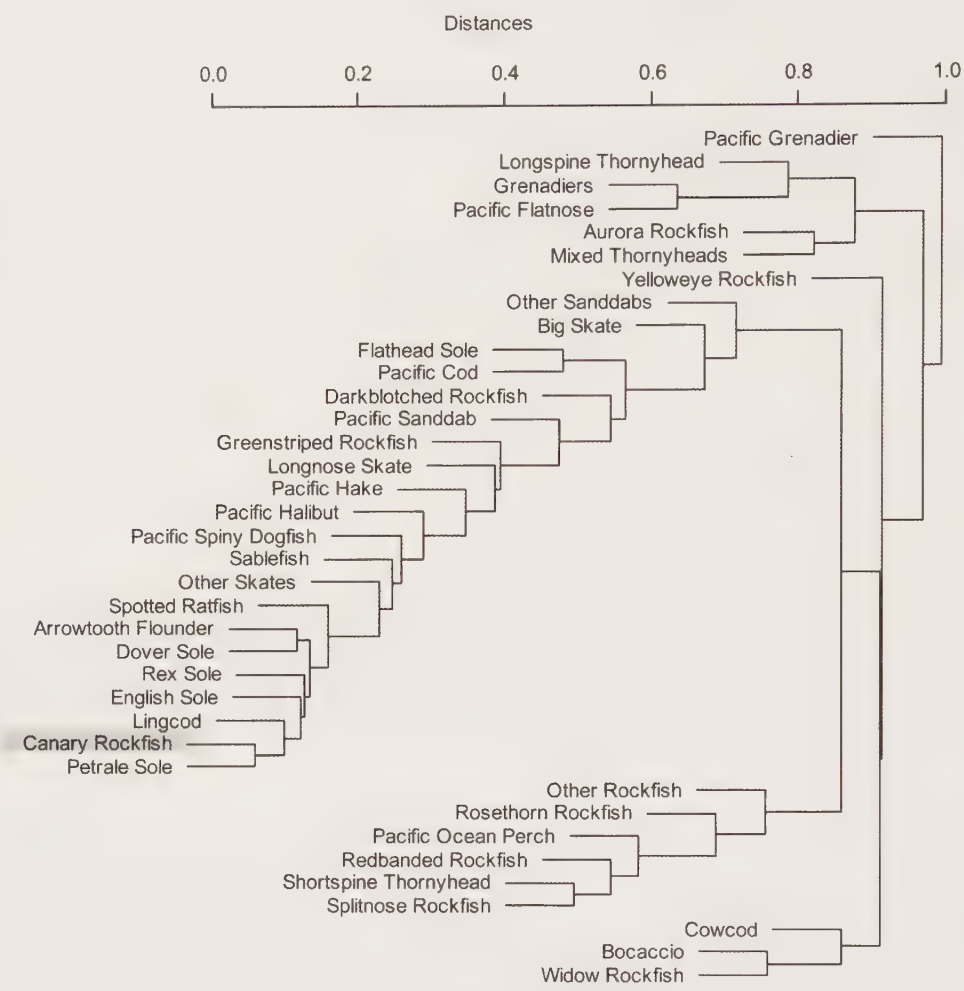

Figure 3

Dendrogram of species clusters determined with hierarchical cluster analysis and based on data from all years, but including only data from tows in which Canary Rockfish were caught. This method was used to evaluate whether clustering could be identified for tows in which rebuilding species were caught. As the figure shows, the method results in a single large cluster of all of the other species that were most common in tows where the rebuilding species of interest were caught. The distance axis represents dissimilarity measures from the cluster analysis.

and Petrale Sole. Sand Sole and Starry Flounder were not included in the current analysis because they occurred on fewer than 5% of observed tows. However, the other components of this assemblage were consistent with our findings. Rogers and Pikitch (1992) identified 2 deepwater assemblages, 1 consisting primarily of Sablefish and Dover Sole, and a second that included Darkblotched Rockfish, Pacific Ocean Perch, Splitnose Rockfish, Yellowmouth Rockfish (*Sebastes reedi*), and Sharpchin Rockfish (*S. zacentrus*). The results presented here were similar when data from port groups along the northern coast were analyzed. These similarities are expected because the data used by Rogers and Pikitch (1992) were collected between 42°60′ and 48°42′ north latitude.

Contrary to the current analysis, Rogers and Pikitch (1992) found that 3 of the rockfish now identified as rebuilding species formed a cluster with other species. Their results show Bocaccio, Canary Rockfish, and Yelloweye Rockfish were part of a nonflatfish shelf grouping that included Yellowtail Rockfish (*Sebastes flavidus*), Sharpchin Rockfish, and Lingcod. In the late 1980s, when the data used by Rogers and Pikitch (1992) were being collected, thousands of metric tons of Bocaccio, Canary Rockfish, and Yelloweye Rockfish were being landed each year. That level of fishing is

Table 4

Species clusters produced by hierarchical cluster analysis and based on data that were stratified into 1° latitudinal intervals. The clusters are shaded or enclosed in solid or dashed lines to make the table easier to read. Group A (light gray), C (dark gray) and G (surrounded by dashed line) represent slope species, and group B (medium gray), D (enclosed in solid lines), E (surrounded by dashed line), and F (surrounded by dashed line) represent primarily shelf species. Only species that formed identifiable clusters were included in the table.

	Latitudinal intervals (in ° North)														
Species	34–35°	35–36°	36–37°	37–38°	38–39°	39–40°	40–41°	41–42°	42–43°	43-44°	44–45°	45–46°	46–47°	47–48°	48–49°
Dover sole	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
Sablefish	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
Shortspine Thornyhead	A	A	A	C	A	A	A	A	A	A	C	A	C	A	
Longspine Thornyhead		A	A	C	A	A	A	A		C	C		C		
Pacific Grenadier										C					
Pacific Halibut											B			A	A
Pacific Cod															A
Petrale Sole	A		B	B	B	B	B		B	B	B	B	B	B	A
English Sole		B		B	B	B	B		B	B	B	F	B	B	A
Lingcod					B	B	B		B	B	B	F		B	A
Bocaccio	B	B													
Sanddabs	B			B						F					
Pacific Sanddab				B						F	B	F			
Spotted Ratfish	A		B	B	D	D				B	A	B	B	B	A
Pacific Spiny Dogfish			B	B		D							A	A	A
Longnose Skate	A	A	B	A	A	D	D	D		A				A	
Skates										A	A				A
Pacific Hake	A	A	B	A	D	D	D	D	A	A	A	A	A		
Rex Sole	A		B	B	D	D	D	D	D	A	A	B	B	B	A
Arrowtooth Flounder					D	D	D	D	D	A	A	A	A	A	A
Splitnose Rockfish	A				D								G	G	
Pacific Ocean Perch													G	G	
Redbanded Rockfish														G	
Greenstriped Rockfish							E								
Canary Rockfish							E								

in stark contrast to more recent fishery trends. Bocaccio, Canary Rockfish, and Yelloweye Rockfish were declared overfished in the early 2000s. Landings of these species, particularly the latter 2 fishes, have since been tightly regulated, and many of the areas where they were known to have been caught have been closed to fishing. As a result of that regulation and of declining population trends, these species were extremely rare in fisheries catch observed from 2002 through 2009.

Despite their rarity, all rebuilding species except for Yelloweye Rockfish formed nonrandom groupings relative to their observed percent occurrence. This finding indicates that even though the ability to predict bycatch of rebuilding species is limited because of their rare occurrence, there may be a possibility to predict species composition specifically from tows where bycatch of rebuilding species occurs. A possible exception may be the Yelloweye Rockfish, which grouped randomly even at low encounter rates. Further research is needed to identify whether bycatch of this species can be tied to other variables beyond species composition.

When all species were included in the analysis, relationships between rebuilding species and other groundfish were not evident at large spatial scales. However, some groupings occurred when data were used from a smaller geographic range. Specifically, rebuilding rockfish formed groups most readily when the data were analyzed separately for each port group. It was difficult to tell whether the clusters formed in these cases were an artifact of error introduced by a smaller sample size, or whether the data were simply isolated temporally and spatially in a way that effectively allowed the recognition of the temporal and spatial structure of species assemblages. The propensity of rebuilding species to form clusters appeared to be a function of sample size. When the subset of data used had a small sample size but included catch of rebuilding species, bycatch of those species became less rare. That said, it is possible that because of the use of departure port, rather than standard latitudinal intervals, to stratify the data, the

Table 5

Species clusters produced by hierarchical cluster analysis with data that were stratified by the departure port of fishing vessels. Different groups were shaded or enclosed in solid or dashed lines to make the table easier to read. Only species that formed identifiable clusters were included in the table. Groups A and B represent the slope and shelf clusters, respectively, which were also evident on a coastwide basis (Table 2). Group C represents the separate slope rockfish assemblage that formed for some northern ports. For some ports, Shortspine Thornyhead and Longspine Thornyhead formed a distinct group, which is represented in the table as Group D. Groups E, F, and G were smaller, distinct shelf species assemblages that were evident in the catch of vessels originating from some ports in Oregon and California.

	Bellingham Bay+ Anacortes	Neah Bay	Westport+Ilwaco	Astoria+Warrenton	Tillamook	Newport	Coos Bay +Port Orford	Brookings	Crescent City	Eureka	Fort Bragg	San Francisco Area+ Bodega Bay	Half Moon Bay	Moss Landing	Monterey +Santa Cruz	Morro Bay	Avila
Sample size (no. of tows)	1375	1044	814	8992	338	3276	2976	647	946	1956	1519	696	859	606	265	728	108
Species																	
Sablefish	A		A	A		A	A	A	A	A	A	A		A	B	A	A
Dover Sole	A	B	A	A	B	A	A	A	A	A	A	A	B	A	B	A	A
Shortspine Thornyhead	A		D	D	D	A	A	A	D	A	A	A	D	A	D	A	A
Longspine Thornyhead			D	D	D	A		A	D	A	A	A	D	A	D		A
Pacific Hake	A		A	A	B	A	A	A	A	A	A	A	B	B	B	A	A
Longnose Skate	A		A	A	B		A	A		A	A	A	B	B	B	A	A
Rex Sole	A		B	B	B	A	A	A	A	A	A	B	B	B	B	B	A
Arrowtooth Flounder	A	B	A	A	B	A	A	A	A	A	A						
Pacific Halibut	A	B	A			B											
Other Skates		B	B		B	A	A								B		
Pacific Spiny Dogfish	A	B	A	A		B		B			B		B	B	B		
Spotted Ratfish		B	B	B	B	B	B	B	B		A	B	B	B	B	B	B
English Sole	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B		
Petrale Sole	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Lingcod	B	B	B	B	B	B	B	B	B	B	B	B	B		B		B
Flathead Sole		B			B												
Pacific Cod	B	B															
Splitnose Rockfish	C		C	C	C		C									B	B
Redbanded Rockfish	C		C	C	C		C										
Pacific Ocean Perch	C		C	C													
Darkblotched Rockfish	C				E												
Greenstriped Rockfish	B				E					F				F	B		
Canary Rockfish	B									F							
Bocaccio														F	B	F	
Cowcod														F			F
Pacific Sanddab					B				B	F		B	B			F	F
Big Skate					B					F							
Pacific Flatnose										G				G			
Pacific Grenadier										G				G			

analysis more effectively identified species assemblages on local fishing grounds that were frequented by vessels from the same port. Indeed, vessels departing from Avila, where Cowcod was closely associated with Pacific Sanddab, appeared to fish within an area typically ranging less than a degree in latitude. Similarly, the range of depths fished by vessels departing from Monterey was typically less than 180 m.

The data used in our analysis were from commercial catches and our results, therefore, reflect species assemblage patterns specifically as they pertain to fisheries. The data and sampling method used in our analyses likely miss finer-scale ecological patterns. Fine-scale ecological information that relates to species occurrences could provide further insight into the association of bycatch and target species, although col-

lection of such information over a spatial scale that matches the fishery would be challenging.

If the same species clusters continue to be identified for each departure port as more data become available, they may provide evidence to support a more localized approach in the data analyses that support fishery management. Currently, bycatch data analyses in the bottom trawl fishery are structured to support managers who are responsible for implementing management measures over a vast area, from northern Washington to southern California (Bellman and Heery, 2013). The measures developed by managers have historically included a combination of trip limits, area closures, gear restrictions, and other approaches (King et al., 2004, Bellman et al., 2005; Branch, 2006). Regulations are often developed through the use of fishery data that have been stratified into a series of smaller management areas. However, even at this level, the measures put in place may be formed on the basis of fishery information from an area spanning hundreds of kilometers and may therefore affect vessels from a variety of different ports (Bellman and Heery, 2013).

This is not to say that large-scale management is ineffective. Fishery managers often rely on bycatch ratios to set bimonthly trip limits and closures of a given area to fishing. Even if species assemblages containing rebuilding and other nontarget species are not evident at the scale being used by managers, the bycatch ratios calculated for these areas should still provide an accurate large-scale representation of bycatch. However, more specific measures that relate bycatch of rebuilding species to catch or landings of a smaller subset of target species may be more relevant if developed through the use of fishery data specific to each port. For instance, bycatch of Darkblotched Rockfish and Pacific Ocean Perch may be more accurately estimated for northern ports by using catch of other deepwater rockfish species as a proxy for fishing effort. However, in other neighboring ports, this relationship with other deepwater rockfish species may not be relevant. For this approach to be effective, more data would need to be collected onboard fishing vessels so that potential species assemblages noted in this analysis can be confirmed and monitored over time. More data have become available since the 2011 implementation of the catch shares program (Toft et al., 2011), which required 100% observer coverage. Localized species assemblages identified from this new, more comprehensive data set, by using the methods presented here, could provide considerable insight to fishery managers as they continue to develop measures aimed at reducing bycatch of rebuilding species.

Conclusions

Data from the West Coast Groundfish Observer Program provided valuable insight into whether there were associations between target and nontarget groundfish species harvested commercially in the west coast demersal trawl fishery. Although many target species formed identifiable clusters, most rebuilding species did not form groupings. This characteristic of rebuilding species may complicate the use of bycatch ratios for fishery management purposes. We used a simulation approach to separate the effect of low rates of occurrence of rebuilding species from the actual tendency of these species to group with target species in cluster analyses. Our findings indicate that, although bycatch relationships between target and rebuilding species offer low predictive potential when coastwide data are used collectively; such relationships may be useful for predicting bycatch for specific port groups or for estimating bycatch amounts on tows when rare bycatch events do actually occur.

Acknowledgments

We are grateful to the fishery observers who have compiled tremendously valuable data through hard work and dedication. We also thank observer program staff for their support, M. Bellman for her central role in the processing of the data used in our study and for providing the map figure, and J. Majewski for the comments and insight she provided for the manuscript.

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In search of climate effects on Atlantic Croaker (*Micropogonias undulatus*) stock off the U.S. Atlantic coast with Bayesian state-space biomass dynamic models

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Abstract—Atlantic Croaker (*Micropogonias undulatus*) production dynamics along the U.S. Atlantic coast are regulated by fishing and winter water temperature. Stakeholders for this resource have recommended investigating the effects of climate covariates in assessment models. This study used state-space biomass dynamic models without (model 1) and with (model 2) the minimum winter estuarine temperature (MWET) to examine MWET effects on Atlantic Croaker population dynamics during 1972–2008. In model 2, MWET was introduced into the intrinsic rate of population increase (r). For both models, a prior probability distribution (prior) was constructed for r or a scaling parameter (r_0); imputs were the fishery removals, and fall biomass indices developed by using data from the Multispecies Bottom Trawl Survey of the Northeast Fisheries Science Center, National Marine Fisheries Service, and the Coastal Trawl Survey of the Southeast Area Monitoring and Assessment Program. Model sensitivity runs incorporated a uniform(0.01,1.5) prior for r or r_0 and bycatch data from the shrimp-trawl fishery. All model variants produced similar results and therefore supported the conclusion of low risk of overfishing for the Atlantic Croaker stock in the 2000s. However, the data statistically supported only model 1 and its configuration that included the shrimp-trawl fishery bycatch. The process errors of these models showed slightly positive and significant correlations with MWET, indicating that warmer winters would enhance Atlantic Croaker biomass production. Inconclusive, somewhat conflicting results indicate that biomass dynamic models should not integrate MWET, pending, perhaps, accumulation of longer time series of the variables controlling the production dynamics of Atlantic Croaker, preferably including winter-induced estimates of Atlantic Croaker kills.

Manuscript submitted 4 September 2012.
Manuscript accepted 27 November 2013.
Fish. Bull. 112:49–70 (2014).
doi: 10.7755/FB.112.1.4

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necesarily reflect the position of the National Marine Fisheries Service, NOAA.

The Atlantic Croaker (*Micropogonias undulatus*) is a demersal sciaenid species common in estuarine and coastal waters of the U.S. Atlantic coast (Chao and Musick, 1977). This species is abundant off the U.S. mid- and southeast Atlantic coast, where it forms a single genetic population and management stock-unit supporting important commercial and recreational fisheries (Atlantic States Marine Fisheries Commission [ASMFC][1]). Exploitation of Atlantic Croaker began in the 1800s, but coastwide (New Jersey–east Florida) commercial removals and bycatch estimates have been consistently reported only since 1950 and recreational harvests and catches since 1981. These statistics show periodic, sudden highs and lows over the time series (Fig. 1A).

Although fishing can have a significant impact on the Atlantic Croaker population (ASMFC[1]; Hare et al., 2010), Hare and Able (2007) advocated the hypothesis that population "outbursts" and harvest variability of Atlantic Croaker are largely driven by long-term trends in winter temperature. This idea was consistent with the observations that juvenile (age-0) Atlantic Croaker spend their first winter (December–March) in estuarine nursery habitats where winter water temperatures appear to regulate juvenile Atlantic Croaker survival and year-class strength (Norcross and Austin;[2] Lankford and Targett, 2001a, 2001b; Hare and Able, 2007; Hare et al., 2010). The mechanistic link between abundance of juvenile Atlantic Croaker and water temperature led Hare and Able (2007) to develop a conceptual model in which sequential warm winters result in high juvenile survival rates. Such high rates of juvenile survival would in turn lead to large year-classes that increase the population size. The reverse would be true of cold winters. These authors found positive, often significant correlations between spring juvenile and adult (age-2) abundances and minimum winter estuarine temperature (MWET) and between coastwide adult catch and either MWET or the North Atlantic Oscillation.

[1] ASMFC (Atlantic States Marine Fisheries Commission). 2010. Atlantic Croaker 2010 benchmark stock assessment. ASMFC, Washington, D.C., 336 p. [Available from http://www.sefsc.noaa.gov/sedar/download/Atlantic%20Croaker%20Stock%20Assessment%20Report.pdf?id=DOCUMENT, accessed January 2012.]

[2] Norcross, B.L., and H.M. Austin. 1981. Climate scale environmental factors affecting year class fluctuations of Chesapeake Bay croaker, *Micropogonias undulatus*. Special Scientific Report 110, 78 p. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA. [Available from http://web.vims.edu/GreyLit/VIMS/ssr110.pdf.]

Their results supported a hypothesis put forward by Joseph (1972) and concurred with the findings of Norcross and Austin.[2] Joseph (1972) analyzed the fluctuations of commercial landings for Atlantic Croaker from the Mid-Atlantic Bight (1890–1967) and discussed 4 possible causes of their sudden decline after 1945 (i.e., recruitment overfishing, habitat degradation by humans, multispecies interactions, and environmental forcing due to natural events). He dismissed the first three causes as potential driving forces of the declining landings and attributed that decline to extremely low winter temperatures that had decimated overwintering age-0 Atlantic Croaker in estuarine nursery habitats. He documented evidence that large landings had been associated with warming of sea temperatures and that the historical declines in landings had always followed cooling trends. On the basis of this information, he originally proposed the overwintering mortality hypothesis in juvenile Atlantic Croaker during cold winters, resulting in weak year-classes and future, low population sizes.

This hypothesis has been repeatedly adopted in subsequent studies. In this respect, Norcross and Austin[2] showed that the abundance of juvenile Atlantic Croaker in Chesapeake Bay (Virginia) during summer positively correlated with estuarine water temperature during the previous winter. They associated the increase in catch in the mid-1970s with warmer winter temperatures and a decrease in catch in the late-1970s with colder winter temperatures.

With the exception of the study by Hare et al. (2010), studies of the population dynamics and management of Atlantic Croaker have ignored environmental effects on the processes modeled (Barbieri et al., 1997; Lee, 2005; ASMFC[3,1]). On the basis of a mechanistic recruitment–winter temperature hypothesis (described above), Hare et al. (2010) developed a coupled climate–population dynamics model. This model is an age-structured production model in which recruitment is generated through a stock-recruit relation, and the age composition is simulated to be conditional on the closest correspondence between predicted and observed harvests. The climate effects are log-linearly incorporated into the model through a Ricker spawning-stock function with a temperature (i.e., MWET) variable. The coupled model indicates that both exploitation and climate changes significantly affect Atlantic Croaker abundance. Importantly, Hare et al. (2010) found a significant correlation between the observed Atlantic Croaker recruitment and MWET, which thereby supports the mechanistic recruitment hypothesis of Hare and Able (2007).

The Atlantic Croaker stock in U.S. Atlantic waters can be considered data-moderate. In fact, this stock has been associated with many data sets, some of which were characterized by considerable uncertainty in their estimates and representativeness. For example, the ASMFC stock assessment subcommittees (ASMFC[3,1]) identified numerous small-scale (i.e., bay- or sound-specific) and 2 large-scale (i.e., spanning wide areas, many years, or both) survey indices of abundance, one coastwide or regional fishery-dependent index (i.e., the total catch per unit of effort [CPUE] from the National Marine Fisheries Service [NMFS] Marine Recreational Fisheries Statistics Surveys [MRFSS]), and various sources of fish kills and length data.

Evaluation of these data sets and assessment procedures revealed the following. The small-scale indices of abundance possibly reflected better local than coastwide dynamics. The first stock assessment (ASMFC[3]) lacked catch-at-age (CAA) data and dealt with conflicting trends in regional indices of abundance. The southeastern (North Carolina–east Florida) shrimp trawl fishery (SESTF) bycatch, commercial fishery discards, and scrap (or bait) fishery landings are currently considered significant but have been poorly characterized. The development of the MRFSS CPUE appeared unreliable and raised concerns about its value as relative index of stock abundance (ASMFC[1]). In this context, differing decisions and assessment choices have been adopted. Preference has been given to large-scale survey indices and, in order to characterize recruitment, to a few small-scale indices developed from survey data collected in the so-called overwintering core area for juveniles. The first stock assessment of Atlantic Croaker (ASMFC[3]) relied on an age-structured production model (1973–2002).

Because of the difficulties encountered in reconciling the conflicts between regional indices, regional models have been developed, thereby splitting the stock into the "northern" and "southern" management units. The model for the south Atlantic region, however, did not perform satisfactorily. Because that portion of the stock could not be assessed, emphasis was placed on the "northern" stock. In contrast, the 2010 assessment subcommittee (ASMFC[1]) did not find evidence to support a north–south separation of the stock and conducted an assessment encompassing data for the coastwide stock. Moreover, this subcommittee developed matrices of CAA for 1988–2008 only and explored various assessment approaches, including continuity runs, but ultimately chose a statistical CAA model that uses the aforementioned CAA data.

The results of that model form the basis for current management. Unfortunately, inadequate estimates of the SESTF bycatch and scrap fishery landings particularly hampered the determination of overfished status of the stock. Meanwhile, various ASMFC stock-assessment subcommittees and review panels documented information about climate effects on the population dynamics of Atlantic Croaker. They consequently recommended that stock assessment models investigate environmental covariates to improve understanding of the

[3] ASMFC (Atlantic States Marine Fisheries Commission). 2005. Atlantic Croaker stock assessment and peer review reports. ASMFC, Washington, D.C, 370 p. [Available from http://www.asmfc.org/, accessed January 2012.]

dynamics in question and management implications. Hare et al.'s (2010) work provides guidance, serving as a preliminary study with respect to the recommendation for age-structured models.

The primary purpose of this study was to investigate whether biomass dynamic models (BDMs) could capture the MWET effects on the population dynamics of Atlantic Croaker off the U.S. Atlantic coast and to determine how this result effected the status determination of the stock. Use of BDMs was aimed to address ASMFC's need and Hare et al.'s (2010, p. 461) suggestion regarding exploration of alternative models incorporating MWET, given that BDMs have the potential to track environmental perturbations (Keyl and Wolff, 2008). Unlike Hare et al. (2010), who dealt only with the "northern" stock of Atlantic Croaker, consistent with ASMFC,[3] BDMs here incorporated relevant data for the coastwide stock in accordance with ASMFC.[1] Analyses relied upon a Bayesian state-space modeling framework with software from the Bayesian inference Using Gibbs Sampling (BUGS) Project.

The influence of MWET on Atlantic Croaker stock biomass and productivity was investigated by two complementary approaches. First, process errors were introduced into a traditional BDM so that it could be determined whether those errors reflected environmental anomalies, assumed here to be largely dominated by changes in winter estuarine temperature (Joseph, 1972; Hare and Able, 2007; Hare et al., 2010) and, hence, showed some relationship with MWET. Second, we investigated the effects of explicitly incorporating MWET into a BDM—that would yield effects on both population dynamics and management parameters.

Materials and methods

Data

This study relied on fishery and survey data used in ASMFC[1] BDMs, except for the MRFSS CPUE because its development was questionable and because it was not considered a reliable index for stock biomass. The fishery-dependent removals (Fig. 1A) included 1) coastwide aggregates of commercial fishery landings and commercial finfish bycatch and discards (1972–2008), 2) coastwide recreational kills (1981–2008), 3) North Carolina scrap landings (1981–2008), and 4) SESTF bycatch (1972–2008).

The NMFS, the Atlantic Coastal Cooperative Statistics Program, and individual state fishery agencies have participated in collecting commercial landings data using various temporal resolutions and reporting requirements and processes. Reported commercial landings for all gear types (including the landed SESTF bycatch) were obtained from the Atlantic Coastal Cooperative Statistics Program Data Warehouse and, in 3 cases, from individual state reports. The commercial finfish bycatch or discards were estimated for gill nets

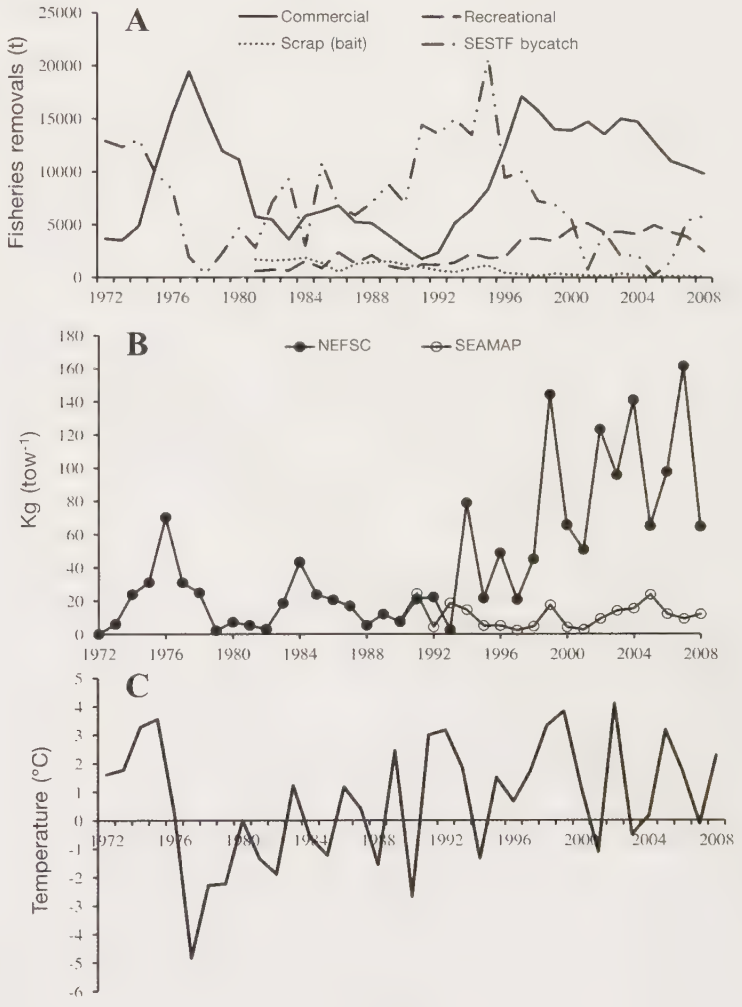

Figure 1

Time series for the period of 1972–2008 of (**A**) commercial, recreational, and scrap (bait) fishery removals and bycatch of the southeastern (North Carolina–east Florida) shrimp trawl fishery (SESTF) for Atlantic Croaker inhabiting the U.S. Atlantic coast; (**B**) biomass indices for Atlantic Croaker inhabiting the U.S. Atlantic coast, specifically the National Marine Fisheries Service–Northeast Fisheries Science Center (NEFSC) fall index and the Southeast Area Monitoring and Assessment Program (SEAMAP) fall index; and (**C**) winter air temperature for Virginia as a proxy for minimum winter estuarine temperature.

and otter trawls by using the geometric mean of the ratios of observed discards to reported landings. These ratios were developed from the NMFS Observer Program data set.

The recreational kills consisted of type A (dead fish brought ashore and available for identification by interviewers), type B1 (fish not brought ashore, hence not seen by samplers, but were used as bait or were discarded dead), and type B2 (fish released alive; they were of small sizes, with a 10% assumed release mortality). They were obtained from data-collection programs operated by the NMFS MRFSS since 1981. Estimates of North Carolina scrap fishery landings were provided by the North Carolina Division of Marine Fisheries, which is the only state agency that routinely sampled such a fishery since 1986 (the 1981–85 estimates were based on the proportion of Atlantic Croaker in the unclassified finfish bait landings during 1986–90).

Atlantic Croaker also are one of the major components of the SESTF bycatch, but the magnitude of the SESTF Atlantic Croaker discards is highly uncertain. The related estimates were produced by using a simple fish-catch to shrimp-catch ratio for study materials collected in North Carolina and South Carolina, and the resulting catch ratio was expanded to the entire coast. Such estimates largely exceeded the reported landings in most years (Fig. 1A) but were considered extremely crude and unreliable. For this reason, ASMFC[1] omitted the SESTF bycatch in BDMs and included them in the age-structured model for sensitivity runs only. Likewise, the SESFT bycatch estimates were used here for sensitivity analyses.

Biomass indices (Fig. 1B) included the fall (September–November) components of the Multispecies Bottom Trawl Survey (1972–2008) of the NMFS Northeast Fisheries Science Center (NEFSC) and the Coastal Trawl Survey (1990–2008) of the multiagency Southeast Area Monitoring and Assessment Program (SEAMAP). The NEFSC and SEAMAP indices were chosen because the corresponding surveys showed wide geographic coverage, temporal coverage, or both; have been conducted consistently; and have provided evidence of regular encounters with Atlantic Croaker of different age groups (ASMFC;[1] Appendix 1). Moreover, unlike the coastwide MRFSS CPUE, the NEFSC and SEAMAP indices were considered reflective of the Atlantic Croaker stock size and trajectory (ASMFC[1]). Although various model runs used the MRFSS CPUE during the 2010 stock assessment, this index raised many concerns and therefore it was excluded from the final assessment model (ASMFC[1]).

MWET was added as a variable of environmental forcing of the Atlantic Croaker population dynamics. Winter air temperature data for Virginia—a Chesapeake Bay region state—were extracted from the website of the Southeast Regional Climate Center (http://www.sercc.com/climateinfo_files/monthly/Virginia_temp.html, accessed May 2012). Air temperature is considered a good proxy for estuarine water temperature because of the efficient ocean-atmosphere heat exchange in estuarine systems (Hare and Able, 2007). On the U.S. Atlantic coast, winter temperatures of one location (here, the Chesapeake Bay region) are a good proxy for the entire coast owing to a strong coherence among local winter temperatures (Joyce, 2002; Hare et al., 2010). As shown in Hare and Able (2007) and Hare et al. (2010), MWET corresponded with the minimum monthly mean air temperature from December to March. Specifically, MWET values were the mean temperatures of the coldest months during the winter seasons. The Chesapeake Bay region's MWET (Fig. 1C) was suited for a study of its effects on the Atlantic Croaker population dynamics because the Chesapeake Bay region is a major overwintering nursery area for the species (Hare et al., 2010).

Biomass dynamic models

The analyses covered the 1972–2008 period, consistent with the years for which data for BDM implementations were available in the 2010 stock assessment (ASMFC[1]). Two Bayesian state-space biomass dynamic models (BSSBDMs) were developed and used: a discrete BSSBDM without MWET (model 1, M1) and a discrete BSSBDM that integrated MWET (model 2, M2). Both models used a one-year time (t) step. A state-space model describes 2 interrelated time series of state and observation processes (Buckland et al., 2004), both of which account for random errors. The state process defined the stochastic temporal dynamics of the unobserved (or latent) age-aggregated stock size of Atlantic Croaker that is due to natural variation. The corresponding error, referred to as process error, is the joint effect of random multiplicative factors (e.g., fluctuations in life history parameters, trophic interactions, environmental disturbance). The process error in M1 included all forms of environmental variations and, in M2, environmental variations over and above the variations pertaining to MWET. The observation errors (arising from measurement and sampling errors) related only to observed indices of biomass. These indices were assumed to be a linear function of the latent biomass.

Consistent with Meyer and Millar (1999) and Millar and Meyer (2000), M1 and M2 described the processes under consideration through a set of 3 probability density functions (PDFs) $g(.)$ and $h(.)$, given the latent, beginning-of-the-year exploitable biomass (B_t), the sets of unknown model parameters ($\boldsymbol{\Theta}$), the set of known covariates ($\mathbf{C}$), and observed indices of biomass by year (O_{it}; i = NEFSC index, SEAMAP index):

$$g_{1972}(B_{1972} \mid \boldsymbol{\Theta})$$

Initial (1972) state PDF (1a)

$$g_t(B_{t+1} \mid B_t, \boldsymbol{\Theta}, \mathbf{C})$$

State PDF (t = 1973, ..., 2008) (1b)

$$h_{it}(O_{it} \mid B_t, \Theta)$$

Observation process PDF
$(i = 1, ..., 2; t = 1972, ..., 2008).$ (1c)

Specifically, $\mathbf{C} = \mathbf{R} \cup \mathbf{W}$; $\mathbf{R} = \{R_t\}$, the set of total fishery removals (t=1972, ..., 2008); and $\mathbf{W} = \{W_t\}$, the set of MWET time series (t= 972, ..., 2008). For M1, B_t was exposed only to fishing ($\mathbf{C} = \mathbf{R}$). For M2, B_t was affected by both fishing and water winter temperature ($\mathbf{C} = \mathbf{R} \cup \mathbf{W}$). For simplicity, the fisheries removals were assumed to be known perfectly. The SEAMAP index during 1972–89 was treated as an unobserved random variable because it was unavailable across that period.

The deterministic, time-discrete part of biomass expectation in M1 and M2 is expressed as

$$E(B_{t+1}) = \hat{B}_{t+1} = B_t + G_t - \sum_f R_{ft}, \quad (2)$$

where f = a subscript for fishery and, during year t;
G_t = production that quantifies the overall change in biomass due to somatic growth, recruitment, and natural mortality; and
R_{ft} = fishery-specific removals.

G_t is a function of B_t, the intrinsic rate of population increase (r), and the carrying capacity (B_∞). The Graham-Schaefer (or logistic) form was chosen to quantify G_t because of its simplicity (it has 2 parameters, r and B_∞) and because it is a central case among possible shapes of production models (Prager, 1994). Therefore, for M1,

$$G_t = rB_t\left(1 - \frac{B_t}{B_\infty}\right). \quad (3a)$$

In biomass dynamic modeling with environmental effects, environmental factors can act on the stock productivity (i.e., on r, B_∞, or both), the fisheries' or surveys' catchabilities, or both (Fréon, 1988; Jacobson et al., 2005; Jensen, 2002, 2005). MWET was normalized and introduced into the parameter r because MWET affects Atlantic Croaker productivity through growth or recruitment during the prerecruit stage (Hare and Able, 2007). The approach followed the framework of log-linearly adding environmental covariates into fisheries models (e.g., Hilborn and Walters, 1992) and assuming implicit controlling effects of MWET on recruitment (Iles and Beverton, 1998; Levi et al., 2003). Therefore, for M2, the year-specific intrinsic rate of increase (r_t) is

$$r_t = r_0 e^{\alpha W_t}, \quad (3b)$$

where α is a coefficient controlling (linearly) the influence of MWET on Atlantic Croaker productivity and r_0 is a scaling parameter. In common with similar applications (e.g., Maunder and Watters, 2003), α was limited to values greater than zero because MWET is positively correlated with juvenile production (Norcross and Austin[2]; Hare and Able, 2007).

To improve the efficiency of the Markov Chain Monte Carlo (MCMC) estimation algorithm implemented in BUGS, the state-space formulations of M1 and M2 were expressed in terms of depletions, b_t ($b_t = B_t/B_\infty$), herein considered to be "true" and assumed to have log-normal distributions (Meyer and Millar, 1999; Millar and Meyer, 2000):

$$b_{1972} \sim LN\left[\log\left(\hat{b}_{1972}\right), \tau_p^2\right]$$

for M1 and M2, (4a)

$$b_{t+1} \sim LN\left\{\log\left[(1+r)\hat{b}_t - r\hat{b}_t^2 - b_\infty \sum_f R_{ft}\right], \tau_p^2\right\}$$

for M1 (t = 1973, ..., 2008),[4] (4b)

$$b_{t+1} \sim LN\left\{\log\left[(1+r_t)\hat{b}_t - r_t\hat{b}_t^2 - b_\infty \sum_f R_{ft}\right], \tau_p^2\right\}$$

for M2 (t = 1973, ..., 2008), (4c)

where $\hat{b}_t$ = the expected depletion in year t, treated as deterministic;
b_∞ = $1/B_\infty$; and
τ_p^2 = the precision (inverse of the variance, σ_p^2) of the process error.

For the observation error model (Eq. 1c), each biomass index (i_{tj}) was assumed to be proportional to the year- and period (j)-specific biomass and to be log-normally distributed about its expected, model estimate ($\hat{i}_{tj}$):

$$i_{tj} \sim LN\left[\log\left(\hat{i}_{tj}\right), \tau_{ij}^2\right] \quad (5a)[5]$$

$$\hat{i}_{tj} = A_{ij}\Phi_t b_t B_\infty. \quad (5b)$$

For the NEFSC index, j=1 (1972–93) when the index varied at low levels with no obvious trend or 2 (1994–2008) when the index showed an overall increasing trend (Fig. 1B). In fact, this index indicates that Atlantic Croaker accessibility and vulnerability changed between these periods. For the SEAMAP index, j = 1 (1990–2008) because the index varied without trend (Fig. 1B). In Equation 5a,

τ_{ij}^2 = the observation error precision ($\tau_{ij}^2 = 1/\sigma_{ij}^2$, σ_{ij}^2 is the observation error variance) by period.

In Equation 5b,

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[4] Equation 4 a–c corresponds with BUGS parameterizations and code. The usual stochastic formulation of Equation 4b, for example, is $b_{t+1} = \left[(1+r)\hat{b}_t - r\hat{b}_t^2 - b_\infty \sum_f R_{ft}\right] e^{\varepsilon_t}$, where $\varepsilon_t \sim N\left(0, \sigma_p^2\right)$ and $(1+r)\hat{b}_t - r\hat{b}_t^2 - b_\infty \sum R_{ft} = \hat{b}_{t+1}$. The expected (deterministic) biomass ($\hat{B}_{t+1}$) and the stochastic (true) biomass (B_{t+1}) in year t+1 are $\hat{B}_{t+1} = \hat{b}_{t+1}B_\infty$ and $B_{t+1} = b_{t+1}B_\infty = \hat{b}_{t+1}B_\infty e^{\varepsilon_t}$. The same formulation applies for Equation 4, a and c.

[5] The usual stochastic formulation of Equation 5a is $i_{tj} = \hat{i}_{tj} e^{\omega_{ijt}}$, with $\omega_{ijt} \sim N\left(0, \sigma_{ij}^2\right)$.

A_{ij} = the stock availability coefficient by period, assumed to reflect all biological and ecological factors affecting the stock;

Φ_i = the survey's global efficiency, assumed to be constant and to measure human and technological factors of the survey while catching animals available in the sampled strata.

The assumption of constant Φ_i implies a time-invariant sampling protocol, which has broadly prevailed for each survey program during the time frame considered. Both A_{ij} and Φ_i modify the survey catchability by period (q_{ij}), which was expressed as $q_{ij} = A_{ij}\Phi_i$. Note that, for each survey, q ranges from zero to one; in other words, $A \in [0,1]$ and $\Phi \in [0,1]$; $q = 0$ if $A = 0$ (unavailable animals during the survey) or $\Phi = 0$ (inefficient survey).

Model parameters, derived quantities, and parameter estimation procedure

The sets of parameters were $\Theta = \left\{r, b_\infty, \sigma_p^2, \sigma_{ij}^2, A_{ij}, \Phi_i, \hat{b}_{1972}\right\}$ for M1 and $\Theta = \left\{r_0, \alpha, b_\infty, \sigma_p^2, \sigma_{ij}^2, A_{ij}, \Phi_i, \hat{b}_{1972}\right\}$ for M2. The derived metrics included $b_{1972},\ldots,b_{2008}$; B_∞; B_{1972}, $\ldots,B_{2008}$ (assumed to follow a lognormal distribution); $SEAMP_{1972},\ldots,SEAMP_{1989}$; q_{ij}; the expected maximum sustainable yield, $\widehat{MSY}$ ($\widehat{MSY} = rB_\infty/4$); the expected biomass and harvest rate at $\widehat{MSY}$ ($\hat{B}_{MSY} = B_\infty/2$ and $\hat{H}_{MSY} = r/2$); the biomass and fishery-specific harvest ratios $B_t/\hat{B}_{MSY}$ and $H_{ft}/\hat{H}_{MSY}$; and for M2, $r_{1972},\ldots,r_{2008}$. The previous metrics for management strictly relate to M1. For M2, $\hat{B}_{MSY} = B_\infty/2$ and the ratio $B_t/\hat{B}_{MSY}$ are still valid, but other metrics are year-specific (Fréon, 1988; for comparable alternatives, see Jacobson et al., 2005; Jensen, 2005) and *de facto* log-linearly related to MWET: $\widehat{MSY}_t = r_t B_\infty/4$, $\hat{H}_{MSYt} = r_t/2$, and the harvest ratio is $H_{ft}/\hat{H}_{MSYt}$. Each fishery-specific harvest rate was estimated as $H_{ft} = R_{ft}/B_t$. The total harvest rates and harvest ratios were calculated similarly, across fisheries.

The BSSBDM parameters were assumed to be mutually independent. The Bayes theorem (e.g., Hilborn and Mangel, 1997) was used to estimate the posterior distributions of the BSSBDM parameters and of the derived metrics or statistics of interest. The use of the Bayes theorem first required specification of prior PDFs, $P(\Theta)$, about knowledge or hypotheses on Θ (Table 1), independent of information contained in biomass indices. The models were then fitted to the observed data of biomass indices (O) by using a likelihood (or sampling density) function, $L(\Theta) = P(O \mid \Theta)$ and, in the process, updated $P(\Theta)$ into the joint posterior probability, $P(\Theta \mid O)$.

A prior PDF was developed for the parameter r only (Appendix 2) on the basis of Atlantic Croaker demographics (Appendix 3). This PDF was applied to both M1 and M2 but stood for r_0 in M2 (Table 1). To aid direct comparison of models, priors for other parameters were specified similarly with noninformative distributions (here gamma, uniform, or normal; henceforth denoted G, U, and N, respectively). Similar to the role played by b_∞ in lieu of B_∞, priors were assigned to $a_{ij} = 1/A_{ij}$ and $\varphi_i = 1/\Phi_i$ to increase the mixing speed and efficiency of the Gibbs sampler underlying BUGS; A_{ij} and Φ_i were derived *a posteriori*. The choice of noninformative priors (Table 1) was dictated by ignorance of most parameters, but those priors have been constrained to fall within bounds suspected to give support to plausible parameter values. For example, B_∞ was assumed to be uniformly distributed between 10× and 100× the observed total fishery removals.

The Gibbs sampler, a MCMC, numerically intensive technique implemented in the WinBUGS software (vers. 1.4.3;[6] Lunn et al., 2000), was used to sample parameter vectors from the joint posterior distributions. WinBUGS was run, without starting values, from R software (vers. 2.15.3; R Development Core Team, 2013) by employing the package R2WinBUGS (Sturtz et al., 2005).

The key issue in MCMC simulations is determination of when the chain has adequately converged (i.e., when the random draws, also called samples, or iterations, truly represent the posterior distribution). In theory, convergence occurs when the number of iterations increases to infinity, but an infinite number of iterations poses problems of computer storage and computing time. Moreover, MCMC samples are characterized by autocorrelation of initial values within the chain. In practice and by convention, convergence can be achieved by lengthening the chain, autocorrelation can be reduced by discarding some initial draws (the burn-in period), and disk space is preserved by keeping one draw every several iterations (thinning). The burn-in period and the thinning interval also must be long.

In this study, 3 independent chains, each with 100,000 iterations, a burn-in period of 50,000 draws, and a thinning interval of 10 (1 in every 10 values was kept) were simulated and led to satisfying convergence diagnostics. Therefore, 5000 iterations for each chain were saved and used for inference. Convergence of MCMC simulations to posterior distributions was checked by inspecting the traces, autocorrelation plots, and Gelman-Rubin (G-R) statistic. In R2WinBUGS, the G-R statistic is called a potential scale-reduction factor or $\hat{R}$ statistic; at convergence, $\hat{R} \approx 1$, 1.1 being an acceptable threshold (Sturtz et al, 2005). This statistic is considered sufficient in most practical situations (Rivot et al., 2004). The final marginal posterior PDFs were summarized in terms of the mean, standard deviation, median, and the 2.5th and 97.5th percentiles, which define the 95% Bayesian central interval (95% BCI). A 95% BCI means that there is exactly a 0.95 probability that the true value of a parameter lies within that interval given the model, data, and priors (Ellison, 2004; Grobois et al., 2008; Kéry, 2010).

[6] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Specifications of the probability density functions (PDFs) of priors for parameters implemented in Bayesian state-space biomass dynamic models: without minimum winter estuarine temperature, MWET(model 1, M1), and with MWET (model 2, M2) for Atlantic Croaker off the U.S. Atlantic coast, 1972–2008. The lognormal, gamma, and uniform prior PDFs are symbolized by *LN*, *G*, and *U*, respectively. Priors are vague except for the parameter r (M1) or the parameter r_0 (M2). Tuning indices were the National Marine Fisheries Service–Northeast Fisheries Science Center (NEFSC) fall index and the Southeast Area Monitoring and Assessment Program (SEAMAP) fall index.

Parameter	Definition	PDFs of priors for M1 or M2
r	Intrinsic growth rate	$LN(-0.756,0.0086)^1$
r_0	Scale factor of the intrinsic growth rate	$LN(-0.756,0.0086)^{1,2}$
α	Coefficient of the linear effect of MWET	$G(0.01,0.001)^2$
b_∞	Inverse of carrying capacity (B_∞)	$U(0.0000005,0.000005)$ $U(0.0000004,0.000004)^3$
σ^2_p	Process error variance	$G(0.01, 0.001)$
$\sigma^2_{NEFSC72-93}$	Observation error variance for NEFSC index, 1972–1993	$U(0.01,1)$
$\sigma^2_{NEFSC94-08}$	Observation error variance for NEFSC index, 1994–2008	$U(0.01,1)$
σ^2_{SEAMAP}	Observation error variance for SEAMAP index, 1990–2008	$U(0.01,1)$
$a_{NEFSC72-93}$	Inverse of the stock availability coefficient inferred from NEFSC index ($A_{NEFSC72-93}$), 1972–93	$U(0.01,10)$
$a_{NEFSC94-08}$	Inverse of the stock availability coefficient inferred from NEFSC index ($A_{NEFSC94-08}$), 1994–2008	$U(0.01,10)$
a_{SEAMAP}	Inverse of the stock availability coefficient inferred from SEAMAP index (A_{SEAMAP}), 1990–2008	$U(0.01,10)$
ϕ_{NEFSC}	Inverse of the NEFSC survey's global efficiency (Φ_{NEFSC}), 1972–2008	$U(0.01,1000)$
ϕ_{SEAMAP}	Inverse of the SEAMAP survey's global efficiency (Φ_{SEAMAP}), 1990–2008	$U(0.01,1000)$
$\hat{b}_{1972}$	The 1972 expected depletion	$U(0.1,10)$

[1] The 25th and 75th percentiles of this prior in arithmetic scale were 0.413 and 0.512, respectively.
[2] Prior for a parameter specific to M2.
[3] When the southeastern (North Carolina–east Florida) shrimp trawl fishery bycatch were included.

Model configurations

Models M1 and M2 consisted of the base-case scenarios when using the prior PDF developed for the parameters r or r_0 and excluding the SESTF bycatch. Sensitivity to M1 and M2 outcomes was performed by using an alternative prior for r or r_0, $U(0.01,1.5)$, and including the SESTF bycatch (also treated as "known") among fishery removals. The prior r or $r_0 \sim U(0.01,1.5)$ has been tested on Whitemouth Croaker (*Micropogonias furnieri*) exploited in southern Brazil (Vasconcellos and Haimovici, 2006) and spans the range of possible r values for marine fish populations (Jensen et al., 2012). Models M1 and M2 configured with r or $r_0 \sim U(0.01,1.5)$ were denoted as M1rU and M2rU, respectively; those models involving the SESTF bycatch were termed M1B and M2B.

A reviewer recommended that a diffuse normal prior centered on 0 for the MWET coefficient (α) would be appropriate. Consequently, an alternative prior $\alpha \sim N(0,0.02)$ was used to examine its effects on inferences and especially on the statistics of model comparison. These models were denoted M2N, M2rUN, and M2BN. For these models, estimates of α were constrained to be greater than –5 and the precision of 0.02 was so chosen to reflect moderate ignorance as advised by Kéry (2010) and Kéry and Schaub (2012).

Model goodness of fit and comparisons of models

The standardized median residuals by year for biomass or depletion ($stdr_t$) and for biomass indices ($std\omega_{ijt}$) were calculated as

$$stdr_t = \left[\log(B_t) - \log\left(\hat{B}_t\right)\right] / sd \Leftrightarrow$$

$$stdr_t = \left[\log(b_t) - \log\left(\hat{b}_t\right)\right] / sd,$$

where sd = the standard deviation of residuals in log-space for biomass or depletion; and
$std\omega_{itj} = \omega_{itj}\tau_{ij}$ with $\omega_{itj} = \log(i_{tj}) - \log(\hat{i}_{tj})$.

Their time trajectories were monitored to check whether the stock biomass or depletion and the biomass indices conformed to the assumed lognormal distributions. Upon visual inspections of their scatter points, normal linear regressions were used to fit their trends.

The Bayesian approach to fitting the linear regressions and assessing their adequacy for the temporal trends in standardized residuals was adapted after Kéry (2010). The adequacy in question was based on the posterior predictive checks as reflected in Bayesian *P*-values and plots of the sum-of-squares for trends in replicated ("perfect") standardized residuals against the sum-of-squares for trends in actual standardized residuals. When a model is adequate for the actual data, about half of the points lie above a 1:1 line on the plot. Equivalently, the Bayesian *P*-value is "close" to 0.5, and values "near" zero or one indicate doubtful fit of the model. Unfortunately, the range of Bayesian *P*-values for a good fit is unclear (Kéry and Schaub, 2012). By analogy to Ono et al.'s (2012) similar statistic, a Bayesian *P*-value of 0.45–0.55 was assumed close to 0.5.

The types of association between various standardized residuals and year were identified on the basis of 1) the signs of the posterior means and medians of the trend slopes, 2) the location of zero in the posterior distributions of slopes (i.e., whether the 95% BCI of these slopes covered zero), and 3) the computation of the probability of decline, P^*. This probability should be "close" to 0.5 (i.e., zero centered at the 95% BCI) for the lack of trend; its larger value (typically approaching one) indicated a negative trend and vice-versa for a smaller value approaching zero. The previous 3 procedures were jointly used to draw pragmatic conclusions because it was unclear what value of P^* indicated that a trend was not strong enough to be considered positive or negative.

The deviance information criterion (DIC) and the Bayes factor (BF) were used to compare various BSSBDMs. Although DIC can be problematic in MCMC simulations, it is the most popular method of a Bayesian model fit and selection that is routinely implemented in the WinBUGS software. Typically, DIC selects among models by trading off goodness of fit and model complexity (Spiegelhalter et al., 2002; Wilberg and Bence, 2008) when competing models are fitted to the same data sets. It is given by

$$\begin{aligned} DIC &= 2\bar{D} - \hat{D} = \bar{D} + p_D, \\ D(\Theta) &= -2\log L(\Theta) - 2\log\left[P(O \mid \Theta)\right], \\ p_D &= \bar{D} - \hat{D}, \end{aligned} \tag{6}$$

where D = deviance (measure of goodness of fit);
$\bar{D}$ = the posterior mean deviance;
$\hat{D}$ = the deviance of posterior means of the elements in Θ; and
p_D = the "effective number of parameters."

The statistic p_D is unstable to estimate, is not an integer, does not necessarily correspond with the number of parameters and, although it should be positive, can even be negative. The latter problem usually arises separately or jointly from ill-specifying priors or an ill-fitting model (data-prior conflict), and is symptomatic of suspicious inferences or of non-normal posteriors of the parameters on which priors have been placed (Spiegelhalter et al., 2002).

The model with the smaller DIC is better supported by the data. In practice, comparisons of models are performed by using the difference in DIC (ΔDIC) among the competing models. As a rule of thumb, ΔDIC>10 indicates models with no support for the model with the higher DIC; if 3<ΔDIC<7, the model with the higher DIC has considerably less support; and ΔDIC<2 indicates lack of substantial differences between models compared. All models with ΔDIC<2 units from the lowest DIC model should receive consideration in making inferences (Spiegelhalter et al., 2002).

The BF comparing how well any two models M_x (associated with the null hypothesis) and M_y (corresponding to the alternative hypothesis) fitted the biomass indices was

$$BF_{yx} = \frac{P(O \mid M_y)}{P(O \mid M_x)}, \tag{7a}$$

where $P(O \mid M)$ = the marginal likelihood for $M \in \{M_x, M_y\}$ and was approximated as (Newton and Raftery, 1994; Kass and Raftery, 1995):

$$\hat{P}(O \mid M) = \left[\frac{1}{S}\sum_{s=1}^{S} P(O \mid \Theta_s)^{-1}\right]^{-1}, \tag{7b}$$

where S = the number of simulations and

$$P(O \mid \Theta_s) = e^{-0.5D(\Theta_s)}.$$

The model that predicted the biomass indices better was considered to have more evidence supporting them and, hence, was preferred. Model preference relied on the guidelines of Kass and Raftery (1995) inferred from the natural log of BF (LBF), $LBF_{yx} = 2\log(BF_{yx})$. Here, $BF_{yx} < 1 \Leftrightarrow LBF_{yx} < 0$ supported M_x; evidence for M_x was considered negligible if $1 < BF_{yx} < 3 \Leftrightarrow 0 < LBF_{yx} < 2$; and $BF_{yx} \geq 3 \Leftrightarrow LBF_{yx} \geq 2$ supported M_y.

The competing models included the same types of fishery removals. However, they differed in whether they included MWET, in the type of priors used, or in whether they included the SESTF bycatch.

Environmental anomalies

Assessing MWET effects on the Atlantic Croaker population off the U.S. east coast relied upon 3 approaches. First, in Equation 4 for M1, M1rU, and M1B, any potential environmental effects were implicitly lumped in the posterior process errors of these models, ε_t ($\varepsilon_t = \log(B_t) - \log(\hat{B}_t) \Leftrightarrow \varepsilon_t = \log(b_t) - \log(\hat{b}_t)$). These errors were expected to be theoretically positively correlated with MWET because MWET is considered to be the dominant environmental factor affecting the population dynamics of the species. The relationship between the posterior process errors and MWET was checked by regressing the credible medians of ε_{t+1}, for year $t+1$,

against MWET recorded from December of year t to March of year t+1, given that 1) juvenile, first-overwintering Atlantic Croaker born in year t recruit during the spring–summer months of year t+1 (ASMFC[1]) and 2) the winter water temperatures prevailing during late year t–early year t+1 determine the t year-class strength and influence recruitment and average biomass in year t+1 (Hare and Able, 2007; Hare et al., 2010).

Second, variability of productivity for the Atlantic Croaker stock in response to climate anomaly was examined by regressing the credible medians of surplus production, G_t ($G_t = B_{t+1} - B_t + \sum_f R_{ft}$), and instantaneous surplus production, ρ_t ($\rho_t = \log[(G_t + B_t)/B_t]$), against MWET, because G_t and, especially, ρ_t are sensitive to environmental change (Jacobson et al., 2001; Mueter and Megrey, 2006). Finally, a linear effect of MWET was considered statistically supported if zero was outside the 95% BCI of the coefficient controlling MWET impacts, consistent with runs of models M2N, M2rUN, and M2BN.

Visual inspections of the scatter points indicated that simple linear regressions were appropriate to fit the relationships between the process error, surplus production, or instantaneous surplus production and MWET. The fitting and adequacy of these regressions, the types of association between the regressed variables, and the linear effect of MWET were determined by the techniques outlined above (see also Grosbois et al., 2008; Wilson et al., 2011).

Stock status

The ratios $H_t/\hat{H}_{MSY}$ ($H_t = \sum_f H_{ft}$) and $B_t/\hat{B}_{MSY}$ were compared with the 1:1 ratio—herein considered a criterion of status determination—to judge whether overfishing was occurring ($H_t/\hat{H}_{MSY} > 1$) or whether the stock was overfished ($B_t/\hat{B}_{MSY} < 1$). The probability that $H_t/\hat{H}_{MSY} > 1$, $P(H_t/\hat{H}_{MSY} > 1)$, and the probability that $B_t/\hat{B}_{MSY} < 1$, $P(B_t/\hat{B}_{MSY} < 1)$, were used to estimate the risks of overfishing and of overfished status, respectively (Jiao et al., 2009). $P(H_t/\hat{H}_{MSY} > 1)$ and $P(B_t/\hat{B}_{MSY} < 1)$ corresponded with the proportions of iterations where the most credible means of $H_t/\hat{H}_{MSY} > 1$ and the most credible means of $B_t/\hat{B}_{MSY} < 1$. The previous risk of overfishing relate to M1, M1rU, and M1B. The risk of overfishing for M2 and its variants was $P(H_t/\hat{H}_{MSY_t} > 1)$. These control rules do not conform to the legal sense used by the NMFS, but they are consistent with the rules considered in the ASMFC[1] BDMs.

Results

Goodness of fit and comparisons of models

The standardized median residuals for stock biomass and biomass indices were comparable and trended similarly across models (Fig. 2). Their credible estimates ranged from −1.8 to 1.2, except for the disproportionate (−5.2 to −4.2) 1972 residuals for the NEFSC index, which indicated excessive overestimation of the corresponding observed values (Fig. 2, C and D). The latter residuals were clearly outliers and were omitted in the residual diagnostics.

The plots of discrepancy checks (not shown) and the Bayesian P-values (0.52–0.55) indicated that the fitted linear regressions were adequate for the trends in various standardized residuals. The negative posterior means and medians of all trend slopes evidenced consistent, negative trends in the residuals. Regardless, at a 0.95 probability, those trends stabilized at zero (i.e., the 95% BCIs of their slopes included zero). Moreover, the probabilities of decline were closer to 0.5 than to one (P^*=0.58–0.74 for biomass, P^*=0.52–0.68 for NEFSC index, and P^*=0.62–0.64 for SEAMAP index; the largest P^*-values were associated with residuals from M1rU and M2rU), and, indeed, the posterior distributions of those slopes were bell-shaped and centered near zero. This result agreed with fair fits of biomass indices that were nearly identical across models (Fig. 3) and indicated that the lognormal distribution was a reasonable assumption for the latent biomass and observed indices.

The means of most parameters were slightly different from the medians owing to right-(or left-) skewed posterior marginal distributions (to conserve space, the related details were not provided but are available upon request). Such distributions were therefore slightly better summarized by the percentiles. For competing models with or without MWET, the posterior means and percentiles of the parameters were of the same magnitude. In comparison with base M1 and M2, M1 and M2 sensitivity runs showed the following aspects about the stock productivity, management benchmarks, and initial depletion. Use of the prior r or $r_0 \sim U(0.01,1.5)$ led to 1) nearly doubling the rate of population increase (note: median r=median $r_0 \approx 0.47$ for base M1 and M2, respectively), $\hat{H}_{MSY}$, and $\widehat{MSY}$; 2) predicting similar posterior medians for B_∞ (≈220,000 t) and $\hat{B}_{MSY}$; and 3) estimating lower (75–78%) posterior medians of the 1972 depletion, $\hat{b}_{1972}$ (note: $\hat{b}_{1972}$ = 0.07 for base M1 and M2).

Inclusion of the SESTF bycatch yielded comparable posterior medians for r, r_0, or $\hat{H}_{MSY}$ but increased the credible estimates of B_∞ and $\widehat{MSY}$ by about 1.27 times and doubled the 1972 depletion (b_{1972}). As a result, for M2 variants in particular, year-specific posterior medians of the parameters r and $\hat{H}_{MSY}$ estimated by using M2rU were nearly twice the medians produced by M2 and M2B (Fig. 4); year-specific $\widehat{MSY}$ from M2B were on average 1.3 times higher than those estimates from M2 but averaged 81% of those estimates from M2rU. It was also observed that, in all models with MWET, the r (and related metric) time series mimicked the MWET trend well, but those time series where the prior $G(0.01,0.001)$ was used for the MWET coefficient α varied less than those time series estimated with the

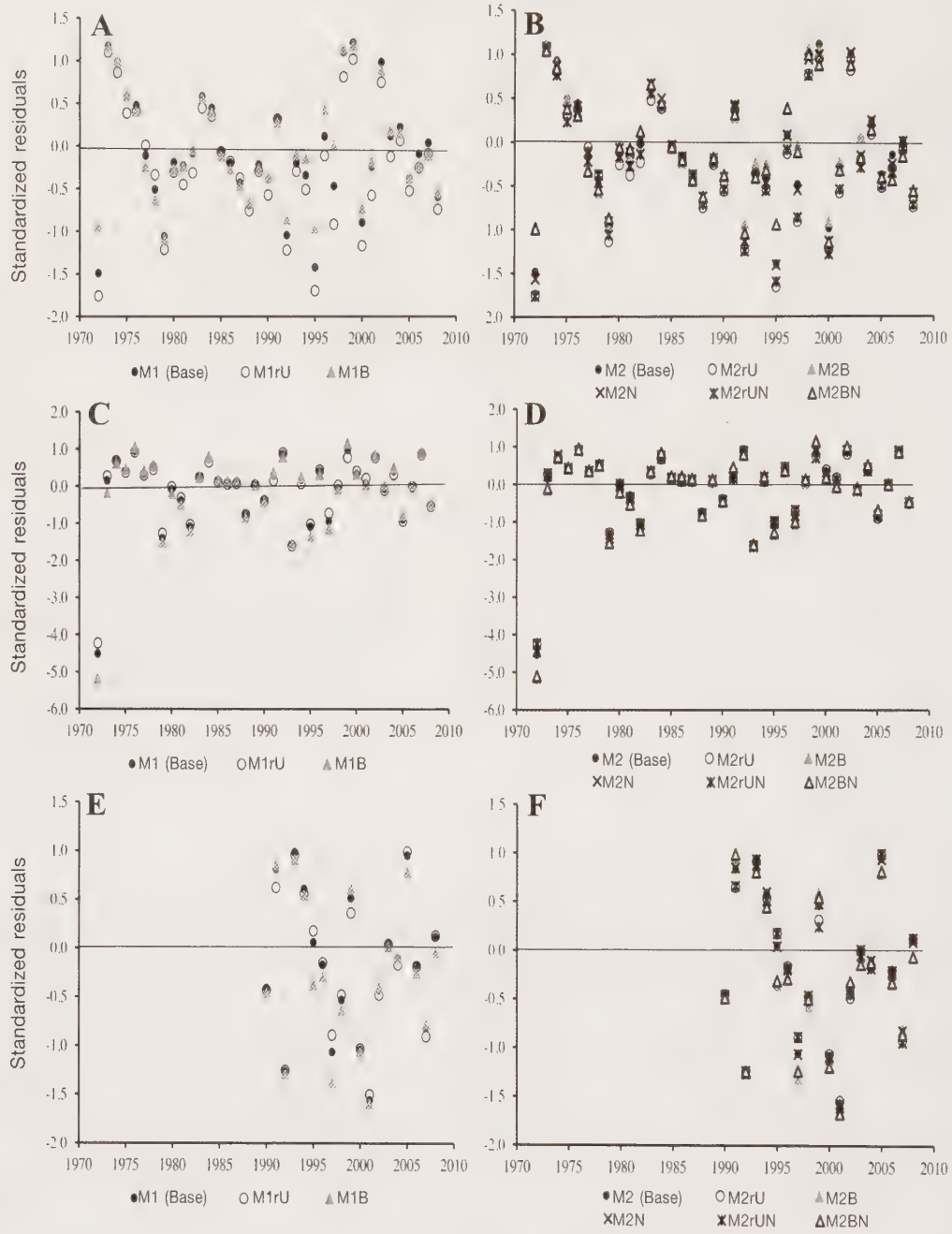

Figure 2

Time series of standardized median residuals for (**A** and **B**) biomass, 1972–2008; (**C** and **D**) the National Marine Fisheries Service–Northeast Fisheries Science Center fall index, 1972–2008; and (**E** and **F**) the Southeast Area Monitoring and Assessment Program fall index, 1990–2008 derived for the Atlantic Croaker stock off the U.S. Atlantic coast by using Bayesian state-space biomass dynamic models: without minimum winter estuarine temperature, MWET (model 1, M1; left panels), and with MWET (model 2, M2; right panels). Residuals relate to model base runs, M1 (Base) and M2 (Base), and to their sensitivity runs: in other words, M1 and M2 using the prior $U(0.01,0.15)$ for the intrinsic rate of population increase r or the scaling parameter r_0, M1rU and M2rU; and M1 and M2 including the southeastern (North Carolina–east Florida) shrimp trawl fishery bycatch, M1B and M2B. M2N, M2rUN, and M2BN are M2, M2rU, and M2B in which the prior for the coefficient controlling MWET effects was centered on zero with a precision of 0.02.

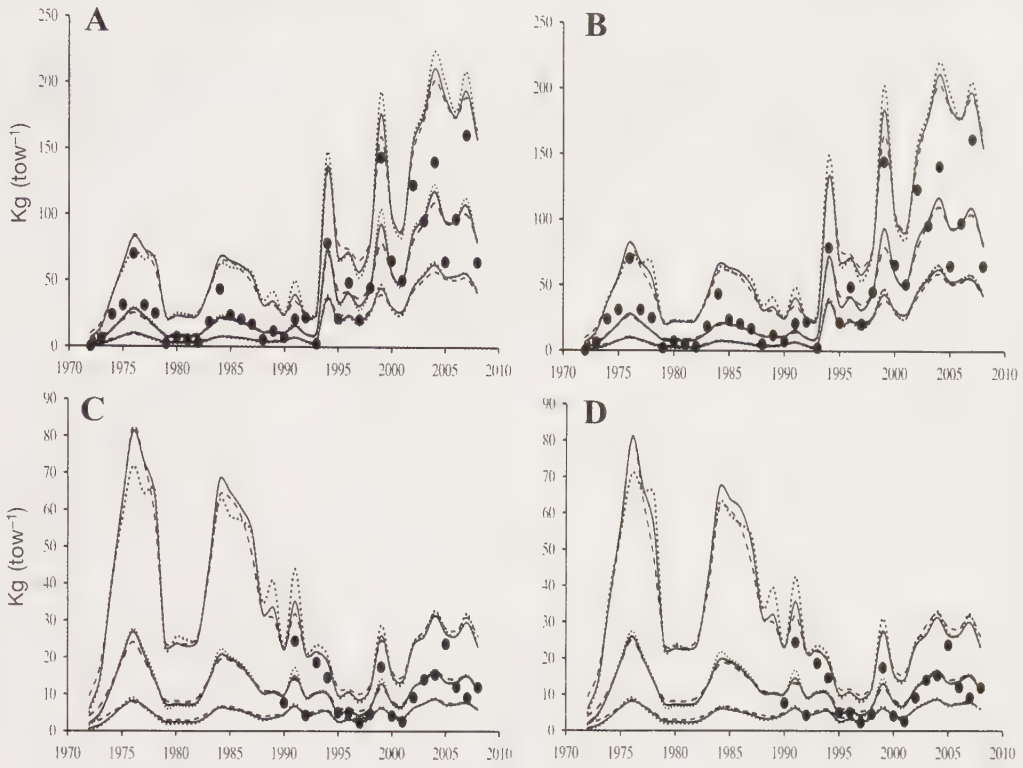

Figure 3

Time series of the predicted posterior medians with 95% central intervals for (**A** and **B**) the National Marine Fisheries Service–Northeast Fisheries Science Center fall index and (**C** and **D**) the Southeast Area Monitoring and Assessment Program fall index for the Atlantic Croaker stock off the U.S. Atlantic coast, derived from Bayesian state-space biomass dynamic models: without minimum winter estuarine temperature, MWET (left panels) and with MWET (right panels), 1972–2008. Filled circles are observed data; solid, dotted, and dashed lines relate to model base runs and model sensitivity runs with the prior $U(0.01,0.15)$ for the intrinsic rate of population increase r or the scaling parameter r_0, and including the southeastern (North Carolina–east Florida) shrimp trawl fishery bycatch, respectively. Models in which the prior for the coefficient controlling MWET effects (α) was centered on zero with a precision 0.02 produced similar credible estimates. These estimated values were not plotted for clarity.

prior $\alpha \sim N(0,0.02)$ (Fig. 4). The stock availability coefficient associated with the NEFSC index (hence, the NEFSC Bottom Trawl Survey catchability) was 8 times higher during 1994–2008 ($A_{\text{NEFSC94–08}}$ = 0.7–0.8) than during 1972–93 ($A_{\text{NEFSC72–93}} \approx 0.11$). The stock availability coefficient, global efficiency ($\approx 1.11 \times 10^{-3}$), and catchability by survey and period were insensitive to model configurations.

The components of the DIC statistics (Table 2) for models without MWET were the NEFSC index, SEAMAP index, depletion time series, and process error variance. They included the coefficient α for models incorporating MWET. Model fits were largely dominated by biomass indices (98–99% of DIC statistics, of which the NEFSC index amounted to 68–73%). The total estimates of p_D were positive and consistent across models, supporting the evidence that all models generally had the same number of parameters.

Other DIC statistics for models of the study were greater for (base and sensitivity) M2 than for (base and sensitivity) M1 and, among model configurations, were the least for M1rU and M2rU. The former result for competing models, with or without MWET, was mainly due to the extra parameter α that clearly had no explanatory power. The DIC associated with α was 4.17 for all M2s and represented 92–101% of ΔDIC (Table 2). For the competing models with alternative priors for the parameter r or r_0, lower DIC statistics for M1rU and M2rU resulted from the decrease in $\bar{D}$ and $\hat{D}$ for biomass indices—a decrease that largely contributed to ΔDIC. This finding indicates an improvement in fit as also evidenced by a slight increase in the corresponding p_D. However, this situation was counterbalanced by

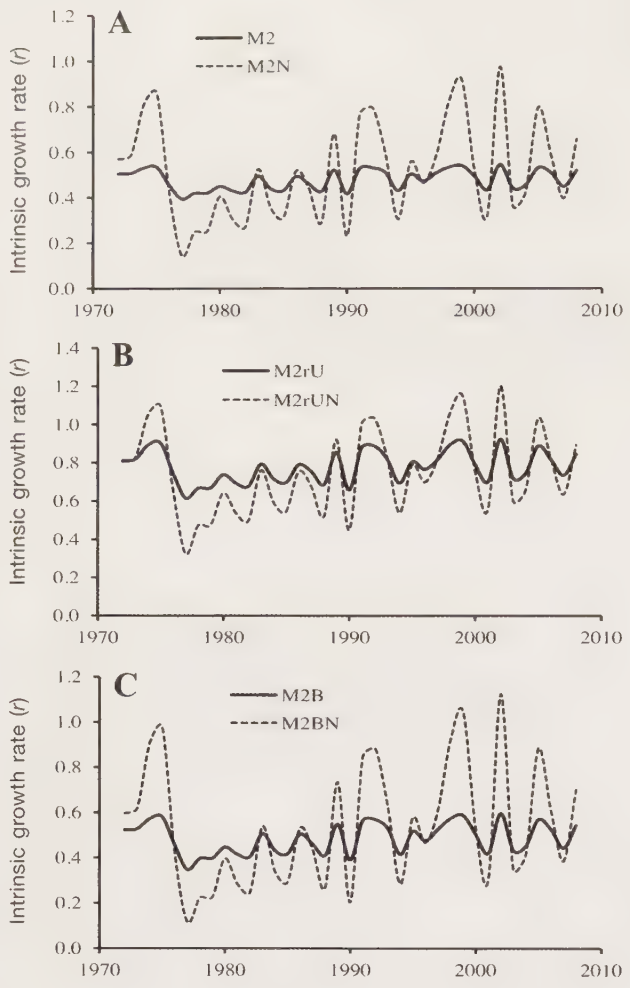

Figure 4

Time series of the predicted posterior medians of the intrinsic rate of population increase (r) for the Atlantic Croaker stock off the U.S. Atlantic coast derived from Bayesian state-space biomass dynamic models incorporating the minimum winter estuarine temperature (M2), 1972–2008. Results relate to (**A**) M2 base runs, (**B**) M2 sensitivity runs with the prior $U(0.01,0.15)$ for the scaling parameter r_0 (M2rU), and (**C**) M2 sensitivity runs with the southeastern (North Carolina–east Florida) shrimp trawl fishery bycatch (M2B). M2N, M2rUN, and M2BN are M2, M2rU, and M2B in which the prior for the coefficient controlling MWET effects (α) was centered on zero with a precision of 0.02. The 95% central intervals of r were not plotted for clarity.

an increase in $\overline{D}$ and $\hat{D}$ associated with the depletion component, with $\hat{D} > \overline{D}$ leading to negative p_D values. This result was symptomatic of an ill-specified (inappropriate?) prior, ill-fitted models, or was symptomatic of both and, hence, of unreliable inferences from M1rU and M2rU runs, although the corresponding overall p_D estimates were positive.

The DIC statistics for M2N, M2rUN, and M2BN did not include negative p_D estimates. On the basis of ΔDIC, they were comparable with those DIC statistics for their counterparts without MWET and, therefore, should be considered for making inferences (Table 2). In short, except M2N, M2rUN, and M2BN, $|\Delta DIC| \in [4.13,5.70]$: models with greater DIC were substantially less well supported despite among-model similarity of residual patterns and magnitude (Fig. 2). (Should the actual deviance for the parameter α be dropped from the DIC for M2, M2rU, and M2B, then $|\Delta DIC| << 2$. This result would indicate lack of differences between models with and without MWET (M1, M1rU, and M1B), and both types of models should be considered for making inferences. However, because α would still have no explanatory power [i.e., the DIC for M2, M2rU, and M2B would still be slightly larger than the DIC for M1, M1rU, and M1B], the parsimonious models [without MWET] would still be preferred). On the other hand, the LBF statistic consistently rejected models with the prior r or $r_0 \sim U(0.01,1.5)$, models incorporating MWET, or both models; even upon some evidence against models without MWET, this evidence was weak (Table 2).

Therefore, comparisons of models indicated that the complexity of (base and sensitivity) M2 brought about by the introduction of MWET was not warranted by the data. Furthermore, the models with the prior r or $r_0 \sim U(0.01,1.5)$ were discredited on the grounds that the values for their depletion component were negative and because of the disagreement between DIC and LBF statistics. Preference was given to results from the LBF statistic for 2 reasons. The BF is among the formal solutions to the model-choice problem (Plummer, 2008). Although Equation 7b is computationally unstable, it is consistent as the simulation size S increases and, in practice, often gives results that are accurate enough for interpretation on the logarithmic scale (Kass and Raftery, 1995). The whole process of model comparisons with DIC and BF (LBF) statistics therefore selected M1 and M1B only. Unless otherwise indicated, the following results related to M1 and M1B.

Extent of climate forcing

The plots of discrepancy checks (not shown) and the Bayesian P-values (0.53–0.55) indicated that the fitted linear models were adequate for the relationships between 1) the process errors and MWET, 2) surplus production and MWET, and 3) instantaneous surplus production and MWET (Fig. 5). These relationships were positive because positive values had most of the mass under the posterior, bell-shaped distributions of their slopes. This result was reflected in positive credible means and medians of those slopes and by large posterior probabilities of increase ($P^* > 0.88$).

Table 2

Results of a comparison of Bayesian state-space biomass dynamic models based on the deviance information criterion (DIC) and Bayes factor (BF) or log Bayes factor (LBF): without minimum winter estuarine temperature, MWET (base model 1, M1), and with MWET (base model 2, M2) for the Atlantic Croaker population off the U.S. Atlantic coast, 1972–2008. Sensitivities to M1 involving the prior $U(0,01,1.5)$ for the intrinsic rate of population increase r and inclusion of the southeastern (North Carolina–east Florida) shrimp trawl fishery (SESTF) bycatch led to models M1rU and M1B, respectively. Sensitivities to M2 involving the prior $U(0,01,1.5)$ for the scaling parameter r_0 and inclusion of the SESTF bycatch led to models M2rU and M2B. M2N, M2rUN, and M2BN are M2, M2rU, and M2B in which a diffuse normal prior centered on zero, with a precision of 0.02, was used as sensitivity to the prior for the coefficient controlling the effect of MWET α. $\overline{D}$ and $\hat{D}$ are mean model deviance and model deviance at the parameter mean, respectively; p_D is the effective number of parameters; ΔDIC is the difference in DIC among competing models. The models compared by using BF and LBF are the same as those models compared by using ΔDIC.

Model	Component[1]	$\overline{D}$	$\hat{D}$	p_D	DIC	ΔDIC	BF	LBF
M1	NEFSC	318.42	308.59	9.84	328.26			
	b_t	0.71	0.51	0.20	0.90			
	SEAMAP	114.79	110.40	4.39	119.17			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	438.95	424.53	14.42	453.37			
M1rU	NEFSC	314.14	304.02	10.12	324.26			
	b_t	1.19	1.28	–0.08	1.11			
	SEAMAP	113.01	108.53	4.48	117.49			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	433.38	418.87	14.52	447.90	M1 vs. M1rU: –5.47	1.02	0.05
M1B	NEFSC	330.48	321.10	9.38	339.86			
	b_t	0.31	0.10	0.21	0.51			
	SEAMAP	117.26	113.65	3.61	120.87			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	453.07	439.88	13.20	466.27			
M2	NEFSC	318.30	308.54	9.76	328.06			
	b_t	0.71	0.46	0.25	0.96			
	SEAMAP	115.17	110.83	4.34	119.51			
	α	4.17	4.17	0.00	4.17			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	443.39	429.05	14.34	457.73	M1 vs. M2: 4.36	1.28	0.49
M2rU	NEFSC	313.66	303.57	10.10	323.76			
	b_t	1.20	1.22	-0.02	1.19			
	SEAMAP	113.49	109.10	4.39	117.88			
	α	4.17	4.17	0.00	4.17			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	437.56	423.10	14.47	452.03	M1rU vs.M2rU: 4.13	0.05	–6.15
						M2 vs. M2rU: –5.70	0.04	–6.59

The process errors from M1 and M1B increased with MWET at a 0.95 probability given that zero was outside the 95% BCIs of the mean slopes (0.133 and 0.124) of the corresponding relationships: those 95% BCIs were (0.017, 0.247) and (0.035, 0.212), respectively. Here, $P^*>0.98$. On average, these relationships explained 14% and 19.5% of the variation in the process errors. In contrast, the 95% BCIs of the slopes for the relationships between surplus production or instantaneous surplus production and MWET included zero. The increase in these productivity metrics with MWET was therefore negligible at a 0.95 probability.

Estimates from M2N, M2rUN, and M2BN of the posterior credible medians of the coefficient for MWET (α) were 0.42, 0.29, and 0.50, respectively, suggesting positive effects of MWET on the Atlantic Croaker production dynamics. However, the related 95% BCIs equaled (–0.57, 1.25), (–0.48, 1.22), and (–0.32, 1.19): these effects were negligible at a 0.95 probability. This result was consistent with that associated with the BF statistic.

Model trends

The biomass ratios, $B_t/\hat{B}_{MSY}$ (Fig. 6, A and B), trended like the depletions (B_t/B_∞; not shown), which themselves tracked the variations of the NEFSC index well. They were characterized by low precision before 1990,

Table 2 (*continued*)

Model	Component[1]	$\overline{D}$	$\hat{D}$	p_D	DIC	ΔDIC	BF	LBF
M2B	NEFSC	330.08	320.71	9.37	339.46			
	b_t	0.28	0.07	0.22	0.50			
	SEAMAP	117.95	114.63	3.68	121.63			
	α	4.17	4.17	0.00	4.17			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	457.52	444.25	13.27	470.80	M1B vs. M2B: 4.52	0.10	-4.51
M2N	NEFSC	317.22	307.33	9.89	327.11			
	b_t	0.82	0.51	0.31	1.13			
	SEAMAP	115.64	111.40	4.23	119.87			
	α	0.55	0.55	0.00	0.55			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	439.26	424.83	14.43	453.69	M1 vs. M2N: 0.32	2.32	1.69
M2rUN	NEFSC	313.96	303.66	10.26	324.22			
	b_t	1.27	1.16	0.11	1.38			
	SEAMAP	113.97	109.69	4.28	118.24			
	α	0.55	0.55	0.00	0.55			
	σ_p^2	5.037	5.037	0.00	5.037			
	Total	434.77	420.12	14.65	449.42	M1rU vs. M2rUN: 1.53	1.76	1.13
M2BN	NEFSC	328.73	319.19	9.54	338.28			
	b_t	0.36	0.09	0.27	0.63			
	SEAMAP	118.23	114.49	3.74	121.98			
	α	0.55	0.55	0.00	0.55			
	σ_p^2	5.04	5.04	0.00	5.04			
	Total	452.91	439.36	13.56	466.47	M1B vs. M2BN: 0.20	2.06	1.45

[1] The components accounted for in DIC calculations for models without MWET were the Northeast Fisheries Science Center (NEFSC) fall index, the Southeast Area Monitoring and Assessment Program (SEAMAP) fall index, the depletion time series b_t, and the process error variance σ_p^2; the components for models incorporating MWET also included the coefficient α. Note that the DIC calculations should only include the components for indices and the depletion, but WinBUGS unexpectedly included the process error variance and α as well.

especially when the commercial removals, the SESTF bycatch, or both suddenly increased. (Following low biomasses in the early 1970s and 1980s, the models predicted large but imprecise depletion levels that were needed to support the upsurge of the fisheries removals). The biomass ratios indicate an overfished stock of Atlantic Croaker in most years except in the mid-1970s, mid-1980s, and perhaps in 1991, 2004, and 2007 when the NEFSC index had peaked after years of low total fishery removals.

The harvest ratios, $H_t/\hat{H}_{MSY}$ (Fig.6, C and D), showed trends opposite of the biomass ratios, and their precision was generally consistent over time. They indicated that the Atlantic Croaker stock likely experienced overfishing during 1993–2001.

The risks for the Atlantic Croaker stock being overfished (Fig. 6, E and F) coincided with the lowest estimates for the NEFSC index and culminated in years when both this index was lowest and the estimates of total fishery removals in the preceding years were highest (e.g., 1972–74, 1978–83, and 1995–2001). This result reflected the model structures and behaviors in that, in a given year, the estimated stock biomass was largely driven by that year's NEFSC index and the total fishery removals of the preceding year. On the other hand, the models interpreted the magnitude of total fishery removals as a signal of overfishing risk: this one was highest in years of larger total fishery removals (1993–2001), lowest otherwise (Fig. 6, E and F). For the period of 2002–08, the risk of overfishing averaged 0.2 and the risk of the overfished status averaged 0.7.

Biomass depletions, ratios, and overfished risks were insensitive to model variants, including the rejected ones, because all models fitted the biomass indices equally. The harvest ratios and risks of overfishing trended similarly across models. In some years, however, the latter statistic was largest for models including the SESTF bycatch.

Discussion

We used BDMs to improve understanding of the climate effects on Atlantic Croaker production dynamics along the U.S. Atlantic coast. An age-structured production model has been applied to address the same

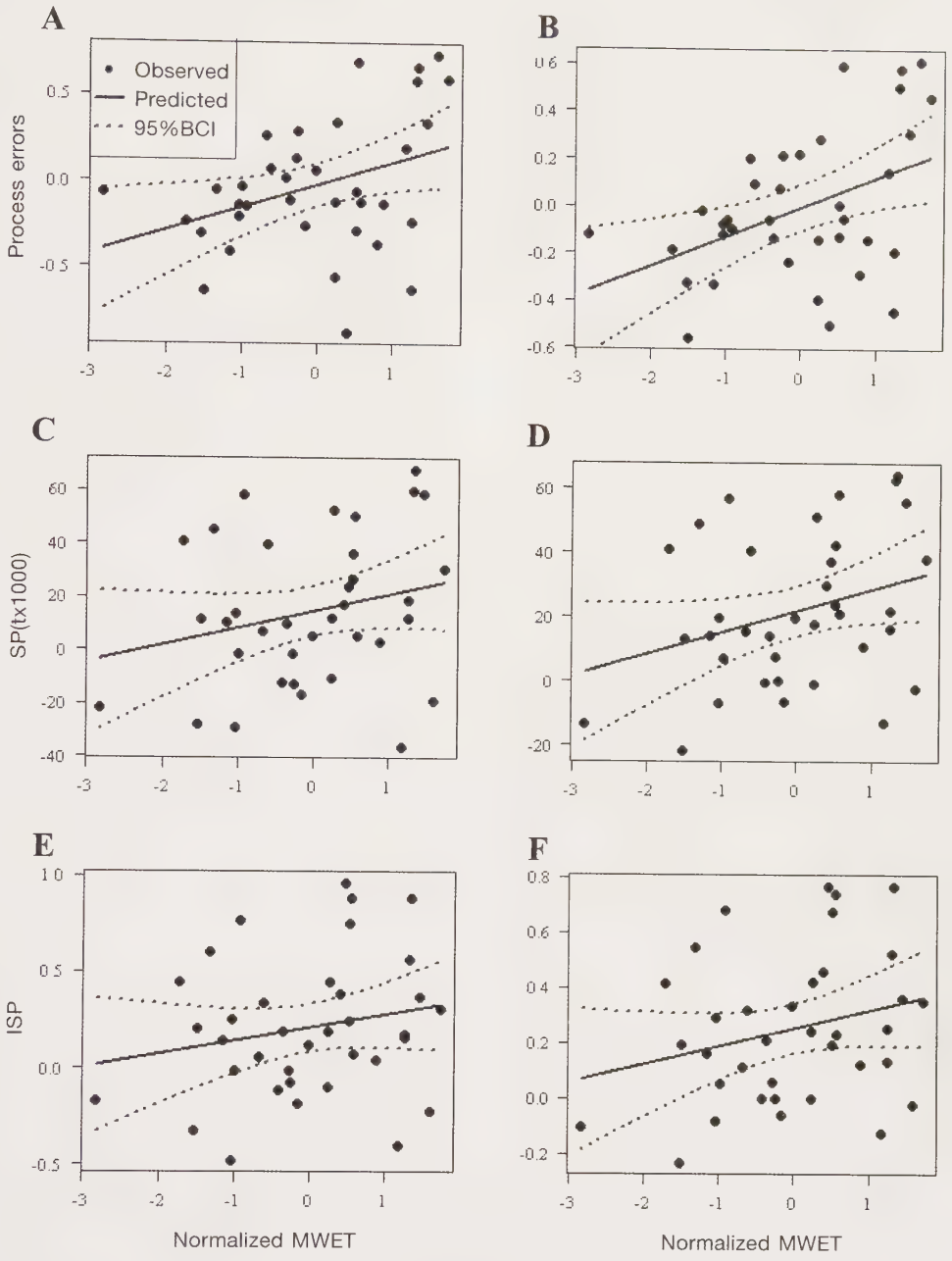

Figure 5

Relationships between the posterior medians of (**A** and **B**) process errors, (**C** and **D**) surplus production (SP), and (**E** and **F**) instantaneous surplus production (ISP) and the normalized minimum winter estuarine temperature, MWET. The process errors, SP, and ISP were generated from the Bayesian state-space biomass dynamic model without MWET (model 1, M1; left panels) and from M1 including the southeastern (North Carolina–east Florida) shrimp trawl fishery bycatch (right panels) for the Atlantic Croaker stock off the U.S. Atlantic coast, 1972–2008. They were treated as observed data. Their fitting with simple linear regressions generated the predicted process errors, SP, and ISP. The insert in panel **A** shows the legend, including for the 95% Bayesian central intervals (95%BCI), common to all plots.

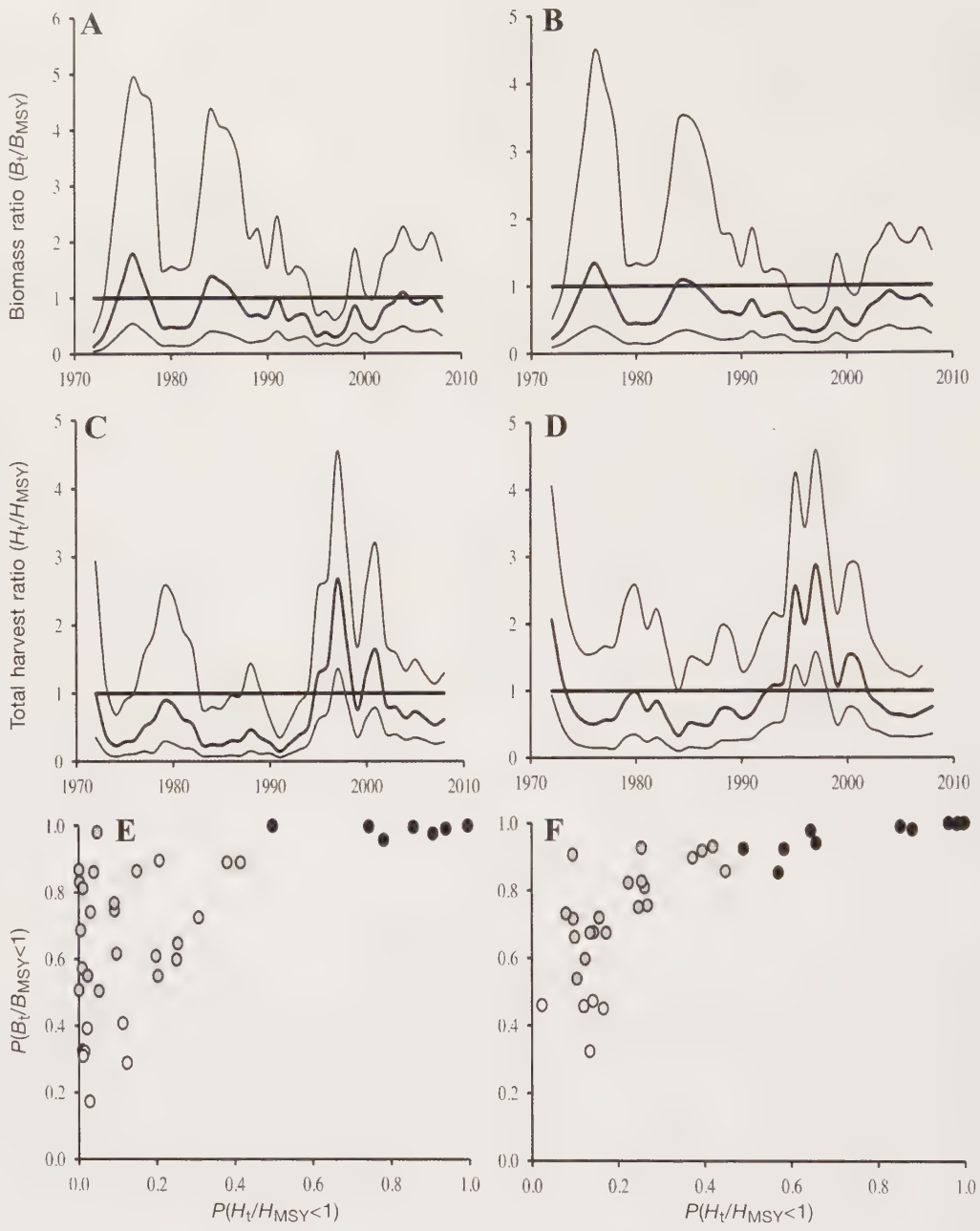

Figure 6

Time series of the predicted posterior medians (thick lines) with 95% central intervals (thin lines) of (**A** and **B**) the biomass ratio and (**C** and **D**) total harvest ratio; (**E** and **F**) plots of the overfished risk, $P(B_t/B_{MSY}<1)$, against the risk of overfishing, $P(H_t/H_{MSY}>1)$, for the Atlantic Croaker stock off the U.S. Atlantic coast. Various stock indicators were derived from Bayesian state-space biomass dynamic models without minimum winter estuarine temperature (model 1 M1; left panels) and from M1 including the southeastern (North Carolina–east Florida) shrimp trawl fishery bycatch (right panels). The horizontal thick line in panels **A**–**D** represents the 1:1 ratio beyond which the stock was considered overfished or experiencing overfishing. In the bottom plots, black circles indicate high overfishing–overfished risks (1972, 1980, and 1993–2001), open circles represent low overfishing–overfished risks (1975–77 and 1984–86), and gray circles correspond to low overfishing risks–high overfished risks (other years).

issue (Hare et al., 2010). However, diversifying investigation models was in part consistent with ASMFC's assessment needs and Hare et al.'s (2010) suggestion for this fishery resource when faced with changes in anthropogenic activity (here, fishing), environmental forcing, and also with parameter uncertainty. BDMs are typically suitable when fishery data are limited to aggregate catch and effort or indices of stock biomass (Hilborn and Walters, 1992; Prager, 1994). Regardless, even in "data-rich" jurisdictions, various stock-assessment teams customarily implement them to support the results of the more sophisticated, data-hungry models. Jacobson et al. (2002) and MacCall (2002) recommended their systematic use as supplemental assessment tools because, in spite of their simplicity and alleged lack of realism, they can be the basis of useful management actions (Ludwig and Walters, 1985; Laloë, 1995).

Investigations have focused on the alleged winter-temperature effects on Atlantic Croaker productivity that occur during the prerecruit stages of the species (Joseph, 1972; Norcross and Austin[2]; Lankford and Targett, 2001a, 2001b; Hare and Able, 2007; Hare et al., 2010). Age- and stage-structured fisheries models are used to investigate environmental effects on population changes through the deviations from an "average" or "virgin" recruitment or through stock-recruitment models, where environmental covariates, along with unexplained random errors, are assumed to influence the recruitment processes and variability (e.g., Iles and Beverton, 1998; Levi et al., 2003; Maunder and Watters, 2003; Hare et al., 2010). These effects can be incorporated into density-dependent, density-independent, or both types of parameters of stock-recruitment models.

By analogy to stock-recruitment models, MWET was introduced into the parameter r that, in surplus-production models, is the counterpart of the density-independent parameter of stock-recruitment models, and process errors characterized all model parameters. Preference was given to the Bayesian state-space modeling framework because of its anticipated flexibility in addressing simultaneously various types of errors and parameter uncertainty and because it was deemed suitable for shedding light on the ability of BDMs to detect MWET effects. A corollary of these investigations was the examination of the extent of such effects on the Atlantic Croaker stock status.

Focusing MWET effects on r was, in conjunction with available fishery data (i.e., fisheries removals and survey indices only), the simplest scenario of implemented BDMs. However, this procedure was also dictated by the need of parsimony in statistical analysis, thereby favoring simple models. If there were supporting data and evidence on changes in habitat conditions—usually affecting B_∞, in other words, the density-dependent parameter (e.g., Jacobson et al., 2005)—or in fisheries effective effort and catchability, it may have also been convenient to consider their effects and interactions on Atlantic Croaker productivity. Information about these factors ultimately needs to be gathered and equally accounted for in future analyses.

The analysis led to mixed outcomes. On the one hand, the positive and significant correlations between the process errors from M1 or M1B and MWET supported the hypothesis that MWET may be playing a role in biomass variability of Atlantic Croaker on the U.S. Atlantic coast. Increased growth or increased recruitment during years of warmer winters would therefore enhance biomass production in subsequent years. However, such relationships were weak in that only 14% and 19.5% of process errors were related to the variation in MWET. On the other hand, there were possible positive relationships between surplus production or instantaneous surplus production and MWET, but the relationships were statistically insignificant. The lack of a relationship between surplus production and an environmental covariate, however, is not unusual.

In contrast, it was surprising that instantaneous surplus production vs. MWET and surplus production vs. MWET exhibited similar and insignificant relationships. Instantaneous surplus production is usually more sensitive to environmental change than is the corresponding surplus production (Jacobson et al., 2001). Likewise, the hypothesis of MWET effects on the Atlantic Croaker production dynamics had no support of the 95% BCIs for the coefficient controlling MWET effects (α) upon specifying its prior as $\alpha \sim N(0, 0.02)$. Weakness and absence of the aforementioned relationships corroborated the fact that BSSBDMs incorporating MWET (although conceptually interesting and ecologically plausible) did not statistically outperform those BSSBDMs without MWET nor did it predict significantly different metrics of stock status. In comparison with Hare et al.'s (2010) results, this study revealed that correlations between MWET and a metric of Atlantic Croaker productivity can appear and disappear or be weak with a modeling approach.

Surplus production models with environmental effects have sometimes improved understanding and description of the performance of fished populations and ecosystems when all key control variables and causal mechanisms have been unambiguously identified, understood, and accounted for (e.g., Fréon, 1988; Evans et al., 1997; Yáñez et al., 2001; Jacobson et al., 2005; Mueter and Megrey, 2006; Thiaw et al., 2009; some contributions in Bundy et al., 2012). Exceptions to such favorable situations exist (Laloë, 1988; Fogarty et al., 2012; this study). Here, BDMs failed to detect MWET effects adequately because of 4 possible major reasons. First, in the process errors–MWET relationships, the remaining, unexplained 81–86% of the variation in the process errors may be rooted in other, yet unknown environmental anomalies. This outcome indicated the possibility that MWET (inter)acted with other ecological factors (e.g., change in other habitat conditions).

Second, random errors and a well-established underlying environmental anomaly may not be linked linearly or may even be unrelated because environmental

fluctuations are not necessarily random (Jensen, 2002; Sinclair and Crawford, 2005). Environmental variations may themselves be driven by other, direct or indirect anthropogenic or natural events, as would have happened for MWET (e.g., Connelly et al.[7]; Fogarty et al.[8]). Third, elusive relationships may have been due to the shortness of the time series for the regressed variables.

Finally, surplus-production models are oversimplifications of the population dynamics in the form of just 2 or 3 parameters (Laloë, 1995; Keyl and Wolff, 2008). Other possible reasons for the blurring or weakening of the impacts of MWET on Atlantic Croaker productivity could be the noisy nature of the tuning indices especially since 1990, the lack of fishing effort that precluded the partitioning of any roles between fishing intensities and MWET, and the functional relationship between the parameter r and MWET. In reality, this function is unknown, and alternative functional forms (e.g., Fréon, 1988; Stenseth et al., 2002; Rose, 2004; Hatton et al., 2006) are conceivable and deserve testing as well.

Overall, the trends generated by this study behaved like those trends obtained through runs of nonequilibrium production models with A Stock Production Model Incorporating Covariates (ASPIC, vers. 5.34. 9, which is included in the NOAA Fisheries Toolbox, http://nft.nefsc.noaa.gov/ASPIC.html) software and Excel spreadsheets (ASMFC[1]). Various implementations of BDMs also produced similar estimates of the initial depletion, MSY, and B_{MSY}, and conveyed a common message that the Atlantic Croaker stock was exposed to a relatively low risk of overfishing in the 2000s. But this analysis showed differences from ASMFC's[1] implementations about the opposing stock status prior to the 2000s (Fig. 6). Contrary to ASMFC's[1] results, this study indicates frequent episodes of overfishing, often with high risks of being overfished, that marked the Atlantic Croaker stock during the period of records. Likewise, overfishing of the Atlantic croaker stock may have been high during 1993–2001 (along with high risks for this stock being overfished) but were low in most years before 1993.

The causes underlying these discrepancies would require dedicated experimental designs for BDM performance analyses, which were not the focus of this study. However, all other things being equal (i.e., no errors pertaining to fishery removals and parameter estimation), the conflicts in the performance of, for example, ASPIC and the BDMs used in this study, can be attributed to model uncertainty (Caddy and Mahon, 1995; Harwood and Stokes, 2003), itself inherently embedded in the general scientific uncertainty (Ralston et al., 2011; Rothschild and Jiao, 2011).

These conflicts may have been jointly or separately rooted in at least 3 major factors. The first factor was the difference in BDM structures (continuous formulation for ASPIC vs. discrete formulation in this study) and the way the corresponding estimation approaches (frequentist vs. Bayesian) dealt with uncertainty. The second factor related to the BDM behaviors resulting from the constrained starting values (ASPIC), nonuse of starting values (this study), and differing estimable parameters. The third and, perhaps, most important (Polacheck et al., 1993; Ono et al., 2012) factor was the error structures assumed including the specifications of the priors' PDFs (observation error for ASPIC vs. observation and process errors in this study). Note that observation errors are year-specific, whereas process errors can propagate over time (Kimura et al., 1996).

This study generated inconclusive, somewhat conflicting results about MWET effects on the production dynamics of Atlantic Croaker. Specifically, these effects were associated with a coefficient without explanatory power or with various linear relationships that proved weak or negligible in justifying addition of a related parameter in BDMs. If BDMs are to be used for assessing the Atlantic Croaker stock, it appears reasonable to continue performing them without considering MWET. Unambiguously discerning the extent of MWET effects through BDMs will perhaps be possible when longer time series of relevant fishery data, winter estuarine temperature (or, preferably, direct estimates of kills caused by cold winter), and other environmental factors will be gathered and accounted for together.

Conclusions

Given the well-established effects of the changes in winter water temperatures on the production dynamics of Atlantic Croaker along the U.S. Atlantic coast, the title of Keyl and Wolff's (2008) article deserves paraphrasing: what can (assessment) models do to track such effects, modify the perception of the stock, and better guide management? The present study has attempted to answer this question through state–space BDMs with and without MWET. BDMs incorporating MWET were not statistically supported by the data and did not outperform BDMs without MWET. The retained BDMs without MWET were associated with process errors, surplus production, and instantaneous surplus production that indicated that MWET had positive effects on Atlantic Croaker productivity. However,

[7] Connelly, W., L. Kerr, E. Martino, A. Peer, R. Woodland, and D. Secor. 2007. Climate and saltwater sport fisheries: prognosis for change. Technical Report Series No. TS-537-07 of the University of Maryland Center for Environmental Science. Ref. No. [UMCES]CBL 07-119. Chesapeake Biological Laboratory, UMCES, Solomons, MD. [Available at: http://www.seasonsend.org/pdfs/Saltwater%20Fisheries.pdf; accessed May 2012.]

[8] Fogarty, M., L. Incze, R. Wahle, D. Mountain, A. Robinson, A. Pershing, K. Hayhoe, A. Richards, and J. Manning. 2007. Potential climate change impacts on marine resources of the northeastern United States. Northeast Climate Impacts Assessments (NECIA). [Available at: http://www.northeastclimateimpacts.org/pdf/miti/fogarty_et_al.pdf; accessed May 2012.]

these effects were statistically significant but weak (i.e., explaining smaller amounts of the variation in the dependent variables) or insignificant, hence negligible. With the available data, BDMs failed to fully capture MWET effects on the Atlantic Croaker population, although these effects are notorious. Accumulation of longer time series of data on fisheries, surveys, winter water temperature, and other relevant covariates (e.g., indices of habitat conditions, winter-induced kills of juveniles), warrant further investigations on BDM performance and their ability to detect cold winter effects on the Atlantic Croaker population dynamics along the U.S. Atlantic coast.

Acknowledgments

This study was prepared under award NA07N-MF470212 from NOAA to the Florida Fish and Wildlife Conservation Commission. M. D. Murphy, J. Boyett, and B. Crowder helped edit this manuscript. W. Cooper and E. H. Leone helped with R programming and appropriate literature. L. M. Lee, K. Drew, and 3 anonymous reviewers offered constructive comments and suggestions. Members of the ASMFC Technical Committee and Stock Assessment Subcommittee for Atlantic Croaker compiled the fishery data and life history information used in this study. This article is dedicated to the memory of my deceased father, Ngendahimana Jean, for having cared deeply about my education despite the fact that he was not formally educated.

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Appendix 1

Characteristics of the Bottom Trawl Surveys of the Northeast Fisheries Science Center (NEFSC), National Marine Fisheries Service, and of the multiagency Southeast Area Monitoring and Assessment Program (SEAMAP) Coastal Surveys[1]. Data obtained from these surveys were used to develop biomass indices for the population of Atlantic Croaker (*Micropogonias undulatus*) off the U.S. Alantic coast during the period of 1972–2008.

Attributes	NEFSC	SEAMAP
Start year	1963	1986
Area coverage	Cape Hatteras (North Carolina, NC)–Cape Cod (Massachusetts)	Cape Hatteras (NC)–Cape Canaveral (Florida)
Targets	Finfish and invertebrates	Finfish, elasmobranchs, sea turtles, invertebrates, and algae
Objectives	Monitor trends in abundance, distribution, and life history traits	Monitor trends in abundance and reproductive conditions
Covariates	Latitude, longitude, salinity, temperature, weather, and hydrographic parameters	Salinity, water and air temperatures, weather, and hydrographic parameters
Design	Stratified random (strata: depth ranges; inshore vs. offshore)	Stratified random (strata: depth contours; depth ranges[2])
Sampling gear	#36 Yankee otter trawl (5-fathom legs; 1,000-lb polyvalent door; 0.5-inch codend liner)	Trawl body: #15 twine and 47.6-mm stretched mesh codend: #30 twine and 41.3-mm stretched mesh codend
Tow duration	30 minutes	20 minutes (daylight hours)
Sampling intensity	Fall (inshore) surveys since 1963; spring surveys since 1968; intermittent summer and winter surveys	Surveys in spring (April–May), summer (July), and fall (October)
Evaluation	Fall surveys regularly encountered Atlantic Croaker since 1972; targeted multiple age classes (0–13 year-old fish)	Most zero tows in spring surveys; only fall surveys were consistent since 1990; targeted multiple age classes (0–6 year-old fish)

[1] Formerly known as Shallow Water Trawl Surveys; conducted by the South Carolina Department of Natural Resources, Marine Resources Division.
[2] Deeper strata (10–19 m) sampled during 1989–2000; abandoned in 2001 to concentrate on shallower depth zones.

Appendix 2

A prior probability distribution was developed for the intrinsic rate of population increase for Atlantic Croaker (*Micropogonias undulatus*) off the U.S. Atlantic coast.

The basic demographics of Atlantic Croaker (Appendix 3) were combined in a Leslie matrix projection framework (McAllister et al., 2001) to construct a prior probability density function for the intrinsic rate of population increase, r (Table 1). The mean reproductive rate-at-age (R_a) was scaled by 10^{-5} to ensure that for all year (50)×replicate (2000) combinations, the resulting r values ranged from 0.01 to 1.5, as seems plausible for marine fish populations (Vasconcellos and Haimovici, 2006; Jensen et al., 2012):

$$R_a = 10^{-5}(p_a SR_a F_a). \quad \text{(A1)}$$

where p_a, SR_a, and F_a are age-specific proportion of mature individuals, sex-ratio (assumed to be 0.5), and mean fecundity, respectively. Implicit in the scaling factor of 10^{-5} for R_a was the assumption that about 11.513 represented the cumulative mortality from egg fertilization to the recruiting age-group (here age-0) in the Leslie population model. Fecundity-at-age was estimated as

$$F_\alpha = \beta\left\{L_\infty\left[1-\exp(-K(\alpha-\alpha_0))\right]\right\}^\gamma, \quad \text{(A2)}$$

where β and γ are parameters of the fecundity (number of eggs)–total length (mm) relationship; L_∞, K, and α_0 are parameters of the von Bertalanffy growth function.

Lognormal distributions were assumed for both natural mortality and reproductive rate-at-age (i.e., they were log-transformed and treated as expected means). Monte Carlo samplings were performed with R software (vers. 2.15.3; R Development Core Team, 2013) with an age-independent coefficient of variation (CV) equal to 0.3 for both parameters (however, a CV=0.3 for the reproductive rate was insensitive to the natural mortality CV $\in$ [0.1, 1.0] in terms of r summary statistics and distributions). The CVs used were a single realization of all possible CV combinations for natural mortality and reproductive rate. They were preferred because, unlike the r estimates in many other trials, the corresponding r estimates fell within and spanned the 0.01–1.5 interval (note: reproductive rate CVs<0.3 yielded truncated r distributions; reproductive rate CVs>0.3 led to r distributions with long tails far beyond 1.5). The stochasticity introduced in natural mortality rates was subsequently propagated into the survival rate and expected survivorship-at-age.

For each replicate, the scalar number for the initial (year-1) population-at-age of female Atlantic Croaker was 1000. McAllister et al.'s (2001) Equations 9–14 or Hammond and Ellis' (2005) Equations 1–5 were applied as appropriate. During the sampling, there were negative values of r. These values usually result from generating stochastic reproductive rates and survivorship values independently of one another, including coupled low values of these parameters, the combination of which can lead to a population that cannot sustain itself (McAllister et al., 2001; Hammond and Ellis, 2005). The final prior probability density function for r (Table 1) was developed after discarding those negative r values and ensuring that the age structure of the projected population was stable (population stability occurred since year-3).

Appendix 3

Demographic inputs for the construction of the prior probability distribution of the intrinsic rate of population increase for Atlantic Croaker (*Micropogonias undulatus*) off the U.S. Atlantic coast. The von Bertalanffy growth parameters are the asymptotic length (L_∞), the growth rate (K), and the theoretical age when length is zero (a_0). The parameters of the fecundity (number of eggs)–length relationship are the coefficient (β) and the exponent (γ).

Attribute	Value or range	Source
Age (a, years)	0–15+	ASMFC[1]
von Bertalanffy growth parameters:		ASMFC[1]
L_∞ (mm)	431	
K (mm×year^{-1})	0.214	
a_0 (years)	−2.35	
Fecundity (F)–length(L) relationship: $F = \beta L^\gamma$		Morse (1980)
β	0.002594179	
γ	3.361	
Maturity-at-age (ages: 0–15+ years)	0, 0.9, 1.....	Barbieri et al. (1994)
Natural mortality-at-age (year^{-1}; age: 0–15+)	0.461, 0.374, 0.324, 0.293, 0.272, 0,257, 0.246, 0.238, 0.232, 0.227, 0.223, 0.220, 0.218, 0.216, 0.215, 0.214	ASMFC[1]

Limited genetic structure of Gulf Menhaden (*Brevoortia patronus*), as revealed by microsatellite markers developed for the genus *Brevoortia* (Clupeidae)

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Abstract—Long-term sustainable management of wild populations should be based on management actions that account for the genetic structure among populations. Knowledge of genetic structure and of the degree of demographic exchange between discreet populations allows managers to better define management units. However, adequate gene loci for population assessments are not always available. In this study, variable co-dominant DNA loci in the heavily exploited marine genus *Brevoortia* were developed with a microsatellite-enriched DNA library for the Gulf Menhaden (*Brevoortia patronus*). Microsatellite marker discovery was followed by genetic characterization of 4 endemic North American *Brevoortia* species, by using 14 novel loci as well as 5 previously described loci. Power analysis of these loci for use in species identification and genetic stock structure was used to assess their potential to improve the stock definition in the menhaden fishery of the Gulf of Mexico. These loci could be used to reliably identify menhaden species in the Gulf of Mexico with an estimated error rate of α=0.0001. Similarly, a power analysis completed on the basis of observed allele frequencies in Gulf Menhaden indicated that these markers can be used to detect very small levels of genetic divergence (F_{st}≈0.004) among simulated populations, with sample sizes as small as n=50 individuals. A cursory analysis of genetic structure among Gulf Menhaden sampled throughout the Gulf of Mexico indicated limited genetic structure among sampling locations, although the available sampling did not reach the target number (n=50) necessary to detect minimal values of significant structure.

Manuscript submitted 14 February 2013.
Manuscript accepted 6 December 2013.
Fish. Bull. 112:71–81 (2014).
doi: 10.7755/FB.112.1.5

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necesarily reflect the position of the National Marine Fisheries Service, NOAA.

Management of wild populations is improved when management actions take into account genetic structure. Stock assessments of marine species are improved when genetic data are used in the development of a fishery stock definition (Begg and Waldman, 1999; Waples et al., 2008). Different outcomes in stock assessments are expected between a scenario with a single exploited population and a scenario in which 2 or more demographically independent populations are exploited simultaneously by a fishery. In the latter case, treating 2 or more independent fishery stocks as a single unit could potentially lead to underestimates of the effects of exploitation on local stocks and an overall diminished yield (Carvalho and Hauser, 1994). Therefore, genetic analyses of population structure can improve stock assessments by increasing accuracy in identification of the number of populations exploited and the extent and direction of demographic exchange (migration) among exploited populations (Begg and Waldman, 1999; Waples et al., 2008).

A recent Southeast Data, Assessment, and Review (SEDAR) stock assessment indicated that more genetic data are needed to appropriately define the stock harvested by the menhaden fishery (*Brevoortia* spp.) in the Gulf of Mexico (Vaughn et al.[1]). Two aspects of the stock definition for the menhaden fishery can be improved with genetic data. First, the menhaden catch in the Gulf of Mexico is thought to consist of 3 species: Gulf Menhaden (*Brevoortia patronus*), Finescale Menhaden (*B. gunteri*), and Yellowfin Menhaden (*B. smithi*). Ahrenholz (1981) suggested that 99% of the catch comprised Gulf Menhaden, but this finding can be re-assessed with sampling of diagnostic microsatellite DNA loci. Second, information about population structure within the species targeted by the fishery, Gulf Menhaden, will result in a better definition of management units that compose the stock (Waples et al., 2008). A more suitable stock definition in turn will result in more practical biological reference points in stock assessments. Previous studies of population structure in Gulf Menhaden have indicated that there is a single stock in the Gulf of Mexico, but these studies were completed with sampling designs that were not specifically intended to assess fine-scale population structure among locales in the Gulf of Mexico (Bowen and Avise, 1990; Anderson, 2007; Anderson and Karel, 2007). A major downfall of these studies has been a paucity of adequate gene loci developed for the genus *Brevoortia*,

[1] Vaughn, D., A. Schueller, J. Smith, and S. VanderKooy (eds.). 2011. SEDAR 27: Stock assessment report, Gulf of Mexico menhaden, 460 p. Southeast Data, Assessment, and Review, Charleston, SC. [Available from http://www.sefsc.noaa.gov/sedar/Index.jsp.]

and this has ultimately resulted in limited resolution in addressing population structure and hybridization among *Brevoortia* congeners in the Gulf of Mexico (Anderson, 2007; Anderson and Karel, 2007; Anderson and McDonald, 2007).

The first step in addressing population structure among wild populations is the identification of appropriate polymorphic loci. Adequate loci with sufficient polymorphism are required to definitively detect patterns of divergence from limited sample sizes. When low levels of genetic divergence have occurred between populations, as might be expected in Gulf Menhaden, the total number of gene loci employed, as well as the average number of alleles across loci, is predictive of the power in detection of that divergence (Kalinowski, 2004; Bernatchez and Duchesne, 2000).

Additionally, gene loci should have a limited amount of extraneous "noise" that can be created by assay-specific genotype errors (for instance, size homoplasy, null alleles, or allele dropout). Many published primer sets intended for use with wild populations generally consist of an initial data analysis from a single, small sample ($n \leq 20$ individuals) and, therefore, may either lack polymorphism or include one or more genotyping inconsistencies that are not identified in the initial marker characterization. Furthermore, primer sets for nonmodel organisms can be difficult to find in the published literature, and the lack of such primer sets commonly results in use of heterologous gene loci from model organisms or ecologically important congeners (Rico et al., 1996). Heterologous loci have been used commonly in nonmodeled organisms, but the genetic variability of these loci in nontarget species is usually lower than the genetic variability in target species (Ellegren et al., 1997) and the evolutionary properties of the repeat motif itself (such as motif sequence or pattern) are unknown.

This study attempts to address the lack of adequate genetic loci for the genus *Brevoortia* generally and for Gulf Menhaden in particular. A genomic library of Gulf Menhaden restriction fragments was enriched for novel short tandem repeats (STRs, or microsatellites), and microsatellite markers were identified by using a published method (Glenn and Schable, 2005). The discriminatory power of the resulting group of microsatellite loci in the Gulf Menhaden population assignment was quantitatively assessed, as was the likelihood of species identification through the use of a subset of diagnostic loci. These loci increase the genetic tools available for improvement of stock definitions in the Gulf Menhaden and other species of *Brevoortia*.

Materials and methods

Study area and sampling methods

Specimens of *Brevoortia* spp. were collected throughout the North American range of this genus and were identified using the morphological characteristics described in Dahlberg (1970). For the initial phase of the study (microsatellite identification), genomic DNA was isolated from 2 Gulf menhaden juveniles (<40 mm total length) collected inshore in the vicinity of Freeport, Texas (Fig. 1) in spring 2012. These individuals were collected with a bag seine along the shoreline. The second phase of the study was carried out with previously sampled individuals from Anderson (2007). These fish included 118 Gulf Menhaden individuals from 4 sampling locales in the Gulf of Mexico sampled between 2002 and 2003: Laguna Madre, Texas, 2003 [n=29]; Matagorda Bay, Texas, 2003 [n=30]; Lake Charles, Louisiana, 2002 [n=29]; and Apalachicola, Florida, 2003 [n=30]). Samples also included 30 Atlantic Menhaden (*Brevoortia tyrannus*) from Sandy Hook Bay, New Jersey, collected in 2002; 8 Atlantic Mehaden from Bogue Sound, North Carolina, collected in 2002; 22 Finescale Menhaden from Sabine Pass, Texas, collected in 2004; and 19 Yellowfin Menhaden from Charlotte Harbor, Florida, collected in 2003. Because these samples were collected across multiple years, it was expected that multiple independent cohorts were collected.

Library enrichment and microsatellite loci cloning

A microsatellite-enriched library of Gulf Menhaden genomic DNA was constructed and microsatellite loci were cloned by using the protocol of Glenn and Schable (2005). Genomic DNA was isolated from 2 juvenile Gulf Menhaden sampled in Freeport, Texas, with a Gentra Puregene Tissue Kit (Qiagen, Inc., Valencia, CA[2]), and DNA was eluted in 50 µL of TE buffer (10 mM Tris, 1 mM EDTA). Each DNA sample was then cut with *Rsa*I restriction enzyme, resulting in fragments in a range of 200–1000 base pairs (bp). Restriction fragments from each sample were then combined into a single pool and ligated to biotin-labeled SuperSNX linkers (Glenn and Schable, 2005). Linked fragments were enriched for microsatellite repeat-bearing fragments with biotin-capture Dynabeads (Life Technologies Corp., Carlsbad, CA) in 2 enrichment mixtures: a trinucleotide mix (AAC, AAG, AAT, ACT, ATC) and a tetranucleotide mix number (AAAC, AAAG, AATC, AATG, ACAG, ACCT, ACTC, ACTG). Successive temperature steps of T_{m1}=48.5°C, and T_{m2}=58.5°C were used for enrichment. Enriched fragments were ligated into plasmids and transformed by using Invitrogen TOPO-TA cloning kits (Life Technologies Corp.), according to the manufacturer's instructions. Transformed bacteria were plated onto 150-mm ampicillin-inoculated S-Gal agar plates (Sigma-Aldrich Co., St. Louis, MO) and grown for 2 days at 37°C. Positive colonies were selected and stored in 50 µL of TE buffer before DNA sequencing.

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA

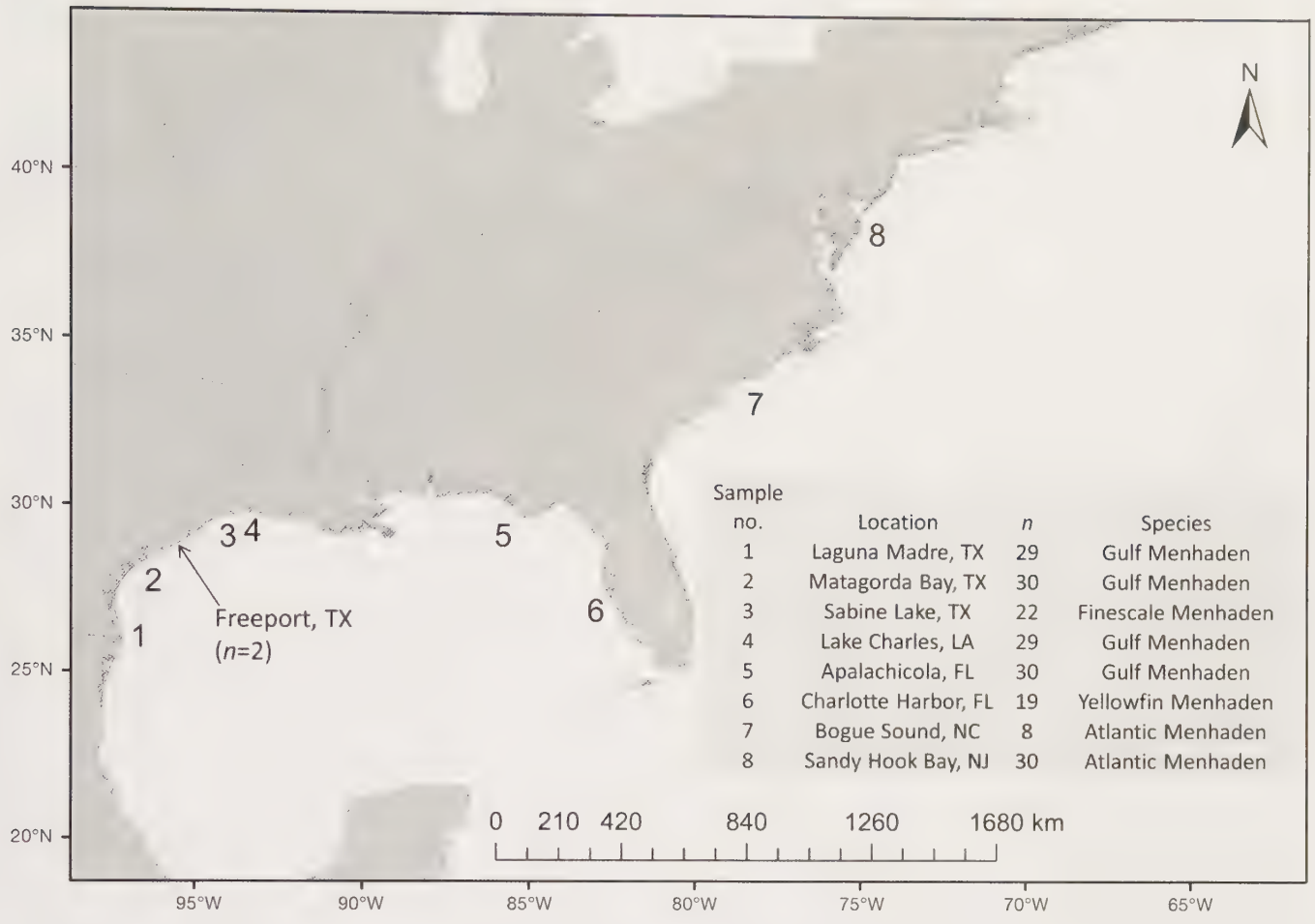

Figure 1

Map of sampling locations in the Gulf of Mexico and Atlantic Ocean where the samples of Gulf Menhaden (*Brevoortia patronus*), Finescale Menhaden (*B. gunteri*), Yellowfin Menhaden (*B. smithi*), and Atlantic Menhaden (*B. tyrannus*) were collected for this study. Samples used for microsatellite identification were collected with a seine net along the shoreline near Freeport, Texas, in 2012. All other samples used for power analysis and analysis of population genetics were taken as described in a previous study (Anderson, 2007) in 2002–04.

Positive colonies were amplified through polymerase chain reaction (PCR) with M13 primers (Life Technologies Corp.) before sequencing. Each reaction included 1 µL of template DNA (50 ng/µL), 1 Ready-To-Go® PCR bead (GE Healthcare Life Sciences, Piscataway, NJ), and 24 µL of forward and reverse primer cocktail (0.4-µM standard primer concentration of each primer), for a total of 25 µL. The following cycling regime was used for PCR: 1) 1 cycle of 2 min at 95°C; 2) 10 cycles of 95°C for 30 s, 55°C for 30 s decreasing 1°C each cycle, and 72°C for 1 min; 3) 20 cycles of 95°C for 30 s, 50°C for 30 s, and 72°C for 1 min, adding 3 s of extension per cycle; and 4) a final extension period of 7 min at 72°C. Aliquots of each PCR product were purified with Exo-Sapit® PCR purification reagent (Affymetrix, Inc., Santa Clara, CA). Purified amplicons were sequenced with M13 primers with the following reaction conditions: 30 cycles of 96°C for 20 s, 50°C for 20 s, and 60°C for 4 min. Sequencing reactions were carried out in 10-µL volumes with DTCS Quick Start Master Mix (Beckman Coulter Inc., Brea, CA) according to the manufacturer's instructions. Sequences were separated with a CEQ 8000 capillary sequencer (Beckman Coulter, Inc.). Raw sequences were trimmed and edited manually and overlapping forward and reverse traces for each sequence were aligned with the software package Sequencher (vers. 4.2; Gene Codes Corp., Ann Arbor, MI).

Primer design and locus characterization

Among 573 positive clones examined, 91 contained repeated fragments, meaning the microsatellite motif was repeated ≥5 times. From the 91 prospective loci, primers were designed for the loci that had the following characteristics: 1) the repeated motif was 3 bases or more in length, 2) no interruptions occurred within

the repeated segment, and 3) at least 20 unambiguously sequenced base pairs were on both sides of the repeated motif, enabling primer design. Primers were constructed manually for the 40 resulting loci, and these primers were used to genotype a panel of 16 Gulf Menhaden individuals (from Matagorda Bay, TX) and 8 Atlantic Menhaden individuals (from Bogue Sound, NC) by using the initial PCR conditions described above. Each primer set was labeled with a WellRed fluorescent dye (primer manufacture and labeling by Sigma-Aldrich Co.), and used to amplify approximately 100 ng of genomic DNA through the use of PCR. Amplified products were combined with a 400-bp size standard and separated with a CEQ 8000 sequencer (Beckman Coulter, Inc.), with default (Frag-1) analysis parameters. Fragment analysis was performed with Beckman Coulter software, and all allelic bins (estimated allele size in base pairs) were established using Beckman Coulter fragment analysis software, with default values for fragment analysis.

The following qualitative criteria were used to choose a final group of microsatellites from the 40 original loci: 1) primer pairs amplified a product in a majority of Gulf Menhaden individuals, 2) alleles were spaced as expected on the basis of the original clone sequences (i.e., trinucleotide motifs were 3 bases apart, tetranucleotide motifs were 4 bases apart), 3) peak intensity appeared to be similar between heterozygote peaks (i.e., there was no visual evidence for allele dropout), 4) alleles were scored with minimum stutter, and 5) preference was given to loci that produced PCR amplicons in both species. This elimination process resulted in 14 loci retained from the 40 original loci examined. An additional 5 loci initially developed for American Shad (*Alosa sapidissima*) (Waters et al., 2000) and previously assayed in *Brevoortia* spp. (Anderson, 2007) were included in the final group to increase the sampling size of the group and to compare the performance of the new loci to a previously published set. All sampled individuals were genotyped by using these 19 loci.

Micro-Checker and genetic polymorphism

The software program Micro-Checker (Van Oosterhout et al., 2004) was used to test each locus for evidence of null alleles and genotyping errors. Each marker was tested independently in all 4 endemic North American species of *Brevoortia*: Gulf Menhaden, Atlantic Menhaden, Yellowfin Menhaden, and Finescale Menhaden. Data from each of the 4 Gulf Menhaden sampling locales also were treated as independent samples and analyzed separately. If evidence was found for a null allele in any sample and locus combination, the frequency of the null allele was calculated as the average of the estimates from 3 independent methods (Chakraborty et al., 1992; Brookfield, 1996; Van Oosterhout et al., 2006). Micro-Checker also was used to assess the statistical likelihood of genotyping errors caused by either allele stutter (one or more PCR artifacts being genotyped as true peaks) or allele dropout (alleles that amplify poorly and, therefore, are not properly genotyped).

The likelihood ratio test of Excoffier and Slatkin (1998) was used to test for linkage disequilibrium between all pairs of microsatellite loci in Gulf Menhaden. Testing was done through the use of the software program Arlequin (vers. 3.5; Excoffier et al., 2005) and statistical significance assessed with 1000 data permutations. The level of statistical significance was adjusted for each comparison of linkage disequilibrium by using the sequential Bonferroni procedure (Rice, 1989). Each marker also was tested for deviation from Hardy-Weinberg equilibrium (HWE), with the expectation that loci with null alleles would likely also deviate from HWE. The exact test method of Guo and Thompson (1992) was used for HWE tests with a Markov chain length of 100,000 steps, as implemented in Arlequin. After the exact test, statistical significance was assessed at each locus with the *P*-value of the test statistic, and statistical significance is reported here both before and after sequential Bonferroni adjustment (Rice, 1989).

The observed and expected heterozygosity and the number of alleles also were estimated for each locus, in each species, with Arlequin. Differences in genetic variability among species were tested by comparing expected heterozygosity (H_e) among species. Each locus was treated as an independent data point, and the null hypothesis that H_e in Gulf Menhaden was not statistically different from H_e in other species of *Brevoortia* was tested with a Wilcoxon nonparametric signed-rank test over all loci. The Wilcoxon test was performed in R software (vers. 2.14.1; R Development Core Team, 2011), with the wilcox.test function. To further compare levels of polymorphism across loci and species, the polymorphic information content (PIC; Botstein et al., 1980) of each marker was estimated from observed allele frequencies in each species. The PIC statistic is a function of both allele number and frequency and, therefore, is a better estimator of discriminatory power than is the number of alleles alone.

The PIC was calculated in R for each locus with the formula

$$PIC_j = 1 - \sum_{i=1}^{n} p_i^2,$$

where p = the frequency of allele i at locus j.

The Wilcoxon nonparametric signed-rank test was used to determine whether Gulf Menhaden had significantly higher PIC scores across all loci than the other *Brevoortia* species.

The relative power of assignment of *Brevoortia* gene loci was tested with the program Whichloci (Banks et al., 2003). The Whichloci method is a resampling technique that generates simulated populations from observed allele frequencies in experimental samples, and then assigns experimental individuals to populations on the basis of the likelihood of an individual's genotype in each population. The accuracy of assignment

can be assessed at any level of assignment stringency, and that level is set by the user as a LOD (log odds) score. Individuals from different samples within species were combined, and the relative power of the loci in the assignment of individuals to species was assessed. Loci that deviated from HWE or that failed to amplify any species were excluded from species assignment. As a result, assignment was performed with 14 loci (see the *Results* section).

During species assignment, marker performance was assessed at various levels of LOD=2, 3, and 4; these levels of stringency are approximately analogous to an acceptable error rate of 0.01, 0.001, and 0.0001, respectively. Simulated population sizes were set at n=100, and 100 replicate simulations were performed. Two properties of the genetic data set were assessed after simulation and assignment: 1) the number of loci needed to correctly assign 100% of individuals to species at the predetermined level of stringency and 2) the relative contribution (locus score; Banks et al., 2003) of each locus in the assignment of individuals when LOD was set at 1. It is anticipated that within the menhaden fishery of the Gulf of Mexico, the Atlantic Menhaden is rarely or never encountered. Therefore, the Atlantic Menhaden was excluded from the analysis.

The power of these loci to reveal small levels of population differentiation within Gulf Menhaden was explored through a POWSIM analysis (Ryman and Palm, 2006). Allele frequencies were estimated from composite data in the Gulf Menhaden samples with Fstat, vers. 2.3, (Goudet, 1995) and were used to perform 500 replicated experiments on 2 simulated populations. Because of the uncertainty involved in accurately estimating and accounting for null alleles, loci that deviated significantly from HWE in Gulf Menhaden and had estimated null allele frequency $p \geq 0.10$ were excluded. As a result, power analysis was performed with 15 loci (see the *Results* section).

The 2-population model was chosen because it is the simplest mode of population structure, and previous studies of marine finfish in the Gulf of Mexico have frequently indicated a marine "suture zone" east of the Mississippi River (Portnoy and Gold, 2012), resulting in eastern and western Gulf of Mexico stocks of several species or species pairs. Two levels of sampling (n=40 and 50 individuals) were conducted after 10 generations of genetic drift, with the assumption of effective population sizes of 500, 1000, and 5000 individuals (these values equate to F_{st}=0.01, 0.004, and 0.001, respectively). The power of the data at each level of N_e and at each sample size was assessed as the number of significant results obtained across all 500 simulations, assessed with the Fisher's exact test.

Genetic structure of Gulf Menhaden

Among the 4 Gulf Menhaden samples, evidence for nonrandom associations of alleles or genotypes (genetic structure) was assessed with the program Structure (vers. 2.3.4; Pritchard et al., 2000). Models that included K=1–4 potential populations were evaluated through comparison of the posterior probability of each model (where K is the prior value for the assumed number of populations represented by the data). Each level of K was assessed with 50,000 burn-in iterations, followed by 450,000 sampling iterations. Prior evaluations of Gulf Menhaden have indicated a high level of gene flow among samples from the Gulf of Mexico; therefore, we used the default Structure model, assuming historical admixture at each level of K, while also assuming allele frequencies among locales were correlated. Admixture coefficient stability among individuals during the course of runs in Structure was used to evaluate model convergence. Loci that deviated from HWE or that had null alleles of estimated frequency $p \geq 0.10$ were excluded from all genetic structure analyses.

Genetic structure was further explored by using the analysis of molecular variance (AMOVA; Excoffier et al., 1992). The initial AMOVA model was used to test for significant genetic divergence among Gulf Menhaden samples (F_{st}), and secondarily among individuals within samples (F_{is}). The significance of variance components in the AMOVA model were evaluated by 1000 permutations of the data, and F-statistics were estimated directly from variance components.

Finally, a Mantel test was used to assess the evidence of isolation-by-distance (IBD) among samples. Geographic association between sampling areas were calculated among sites by using shortest linear shoreline distance. This distance was correlated with Slatkin's linearized F_{st} (Slatkin, 1995) by using the Mantel test. The significance of the coefficient of matrix correspondence (r) was assessed by 1000 permutations of the data. The Mantel test and permutation procedure were conducted with Arlequin.

Results

The original 40 loci that were examined by means of the microsatellite discovery phase have been deposited in the National Center for Biotechnology Information Genbank database (accession numbers KC331110–KC331149). The 14 loci that were retained from the 40 original loci through the use of qualitative criteria are listed in Table 1, and they will be discussed hereafter, along with 5 previously described loci (Waters et al., 2000). Among this final group of microsatellites, there were 6 tetranucleotide repeats, 9 trinucleotide repeats (1 trinucleotide repeat was initially described in Waters et al., 2000), and 4 dinucleotide repeats (all dinucleotide repeats were initially described in Waters et al., 2000). Two of the tetranucleotide repeats unexpectedly contained alleles that were 2 bases apart (BP017, BP039). These alleles were not sequenced directly, but, in both cases, there were very short dinucleotide repeats adjacent to the targeted tetranucleotide repeats in the original clone sequence. It is likely that, in both

Table 1

Locus name, primer sequences, microsatellite motif, and expected product length (in base pairs) for the 14 novel microsatellite loci developed from a Gulf Menhaden (*Brevoortia patronus*) genomic DNA library. The library was constructed using two individuals collected with a bag seine along the shoreline near Freeport, Texas, in spring 2012. Each locus has a GenBank accession number that can be accessed at the National Center for Biotechnology Information (www.ncbi.nlm.nih.gov; accessed 16 December 2012).

Locus	Forward primer	Reverse primer	Motif	Expected PCR length	GenBank accession number
Bp003	ACTGCATGGTCACTAGCACT	CACCACTGCACCGCAGCATGCTGTC	(CAGA)9	170	KC331110
Bp017	CATTTGGATCAAGAGTATCTATCC	CATTCTGCCACACCTCACATAGG	(TCTG)5	150	KC331112
Bp039	GCGTTGACGCGGAGTAATGATCCAG	GATCTCGACTGACTTACAATGCGGC	(GTGA)6	220	KC331113
Bp121	ACTCAAAAGGGCCTGTCTCACGGAG	GCTGATTATAGTCTATAGGTTGGAC	(TCTA)19	200	KC331117
Bp155	GAACTAGCATGGCAGCTAGATCTAG	GAACCATCAGAACAACTCAACCTGC	(ATC)13	150	KC331119
Bp221	TATTGCTGAGCCTGCTTGGCAG	GCCAAGCTGCTGCAGTCCCAGCAGG	(GTT)19	210	KC331123
Bp230	CCAAGGACACATGCCCATATGTCTC	GTCTTCTGAATGGACCGAGTCTGGC	(TCA)16	150	KC331124
Bp239	CAATTTGTGAATCTCCAGGTCAG	GAACGCCAATCACAGCCTGGCAGTG	(CAA)19	160	KC331127
Bp275	TTACGCGCCTGGTGTAGCCTAGCTC	CCTACGTGCGGCTCACATGTCTGG	(ATCAGA)9	170	KC331130
Bp301	CATTATAGCTACAGAGCGGCTGG	CTGAGTGGGGTTCACCGCAGTCTG	(GATA)12	150	KC331134
Bp473	CGGCACTCCGTGAACACAGCGG	ATGTGCTCTTTGGCTGCAG	(CACT)8	170	KC331144
Bp489	AGCGAGGTGAATGGTTCAATTCCAG	GCAAAACAATTGCCCATACTGGGAC	(TAG)10	250	KC331145
Bp501	ACTCTCGCTGTGTTATTGACAGCGC	TCAGTTGACTGTGATCTCATGCGAC	(ATT/GTT)15	150	KC331146
Bp531	CAGGTCTTTGTGACATGCCAAGCTG	CTGACTGCTTGAGGGATCGCAGCAG	(ATG/GTG)16	140	KC331148

cases, the 2-base alleles reflect variation in the untargeted sequence adjacent to the targeted repeat motif. All alleles at these loci were nevertheless scored unequivocally through the use of Beckman Coulter fragment analysis software, and they were treated as dinucleotide repeats in downstream analyses.

In all 4 samples of Gulf Menhaden, 3 of 19 loci revealed evidence of null alleles (Table 2). These loci were BP017 (overall null allele frequency p_n=0.17), BP301 (overall null p_n=0.25), and AF039660 (overall null p_n=0.30). The loci BP301 and AF039660 also showed evidence of genotyping errors due to excessive stutter in multiple populations. Four remaining loci revealed evidence of null alleles in at least 2 populations: BP155 (overall null p_n=0.05), BP239 (overall null p_n=0.03), BP275 (overall null p_n=0.06), and AF039661 (overall null p_n=0.10). A final 2 loci (AF039658 and AF049462) revealed evidence of null alleles at very low frequency (p_n<0.05) in single populations.

The locus BP155 failed to amplify in samples of Atlantic Menhaden, Finescale Menhaden, or Yellowfin Menhaden. There was evidence for null alleles in Atlantic Menhaden at the loci BP017, BP230, BP239, BP301, AF039658, AF0399660, and AF049462 (Table 3). In Finescale Menhaden, 2 loci showed evidence of null alleles (BP301, AF039660). In Yellowfin Menhaden, there was evidence of null alleles at only a single locus, BP301.

Within Gulf Menhaden, there was no evidence for linkage disequilibrium between any pair of loci. Across all loci, there was a range of 6 observed alleles (BP489, AF039661) to 26 observed alleles (AF049462), with a mean of 14.8 alleles per locus (Table 2). When loci that had null alleles were included, there was an average observed heterozygosity of H_o=0.64, and an average expected heterozygosity of H_e=0.74. With null loci removed, both observed and expected heterozygosity averaged H=0.71. Eight loci deviated significantly from Hardy-Weinberg expected genotypes before Bonferroni adjustment. Each of these disequilibrium loci indicated evidence of null alleles. After Bonferroni adjustment, only 4 loci significantly deviated from HWE. These 4 disequilibrium loci (BP017, BP301, and AF039660, AF039661) also had the highest estimated null allele frequency among all loci examined (p_n≥0.10 in each case).

Within other species of *Brevoortia*, overall genetic variability was greatly reduced, in comparison to Gulf Menhaden, for the genetic loci examined. The mean expected heterozygosity was H_e=0.63 in Atlantic Menhaden, H_e=0.37 in Yellowfin Menhaden, and H_e=0.44 in Finescale Menhaden. Heterozygosity across all loci was significantly higher in Gulf Menhaden than in the 3 *Brevoortia* congeners on the basis of the Wilcoxon test (P<0.001, in each case). The mean PIC values for Atlantic Menhaden, Yellowfin Menhaden, and Finescale Menhaden were 0.617, 0.356, and 0.429, respectively (compared with a PIC value of 0.734 for Gulf Menhaden). The PIC value across loci was significantly higher in Gulf Menhaden than in any of the other 3 *Brevoortia* species on the basis of the Wilcoxon test (P<0.001, in each case).

Table 2

Statistics for 19 polymorphic microsatellite loci in Gulf Menhaden (*Brevoortia patronus*) collected throughout the Gulf of Mexico in 2002–04. The statistics include the overall number of alleles observed; heterozygosity, both observed (H_o) and expected (H_e); P-value of Hardy-Weinberg equilibrium (HWE) exact tests; null allele presence and frequency; and polymorphic information content (PIC). Statistical significance of the HWE *P*-value (initial α=0.05) was assessed before (*) and after (**) sequential Bonferroni correction. Loci in italic type were described originally in a study of American Shad (*Alosa sapidissima*) (Waters et al., 2000).

Locus	Alleles	H_o	H_e	HWE (*P*)	Null alleles	Null freq.	PIC
Bp003	15	0.627	0.690	0.227	no	na	0.687
Bp017	10	0.364	0.666	0.000**	yes	0.17	0.664
Bp039	7	0.653	0.613	0.081	no	na	0.611
Bp121	15	0.847	0.851	0.794	no	na	0.847
Bp155	16	0.778	0.892	0.017*	yes	0.05	0.888
Bp221	17	0.847	0.850	0.663	no	na	0.846
Bp230	17	0.863	0.908	0.149	no	na	0.905
Bp239	21	0.838	0.935	0.014*	yes	0.03	0.931
Bp275	24	0.763	0.919	0.017*	yes	0.06	0.915
Bp301	12	0.414	0.867	0.000**	yes	0.25	0.863
Bp473	7	0.615	0.624	0.077	no	na	0.622
Bp489	6	0.085	0.099	0.213	no	na	0.098
Bp501	15	0.907	0.883	0.713	no	na	0.880
Bp531	19	0.915	0.907	0.711	no	na	0.903
AF039657	15	0.686	0.690	0.916	no	na	0.687
AF039658	21	0.763	0.868	0.101	yes	0.03	0.865
AF039660	13	0.271	0.666	0.000**	yes	0.30	0.663
AF039661	6	0.102	0.138	0.001**	yes	0.10	0.137
AF049462	26	0.831	0.930	0.011*	yes	0.02	0.926
Overall	14.8	0.641	0.737	–	–	–	–

Species assignment was carried out with 14 genetic loci, excluding the 4 loci that deviated from HWE in Gulf Menhaden after Bonferroni adjustment (BP017, BP301, AF039660, and AF039661) and also excluding the locus that did not amplify a product in species other than Gulf Menhaden (BP155). Ten of the 14 loci contributed more than 95% to the cumulative locus score in species assignment (Table 4). Interestingly, the microsatellite that ranked highest in species assignment (AF039657) was initially developed for use in American Shad (Waters et al., 2000). With a stringency of LOD=2, 3 genetic loci were required to accurately assign all individuals to species. This number increased to 6 loci at LOD=3, and all 14 loci at LOD=4. At each level of stringency, 100% of individuals were correctly assigned to species.

The Powsim analysis of Gulf Menhaden was conducted with 15 loci and excluded the previously mentioned loci that deviated from HWE and had high null allele frequencies (BP017, BP301, AF039660, and AF039661). At an effective population size of 500, significant genetic divergence among populations was detected in all 500 simulations after 10 generations of drift (F_{st}=0.01), with both sample sizes. At an effective population size of 1000 (F_{st}=0.004), significant genetic divergence was detected in 91% (454/500) of simulations with a sample size of 40 individuals and in 96% (480/500) of simulations when n=50. At the lowest level of genetic divergence (F_{st}=0.001), only 16% (78/500) of simulations resulted in a significant genetic divergence result when n=40 and 22% (112/500) of simulations had that result when n=50.

Analysis of genetic structure of Gulf Menhaden was conducted with the same 15 loci that were used in population assignment (excluding HWE deviating loci). There was little evidence for significant genetic structure among the 4 Gulf Menhaden samples. The Structure analysis indicated that K=1 was the most likely number of genetic clusters represented in the sample (posterior probability P>0.999). When individual admixture scores for levels of K>1 were examined, all individuals were approximately equal admixtures of all 4 genetic clusters. Such a finding is expected in the case of no genetic structure, and in such cases the admixture summary statistic (α) can vary greatly during the course of Structure runs (Pritchard et al., 2000). The AMOVA results similarly indicated a lack of genetic structure among samples (F_{st}=0.002, P=1.0), but there was a small but significant amount of structure among individuals within samples (F_{is}=0.052, P<0.001). A post hoc examination of locus-specific F_{is} indicated that 6 loci of the original suite of 15 loci had significantly

Table 3

Statistics for 19 microsatellite loci examined in Finescale Menhaden (*Brevoortia gunteri*), Yellowfin Menhaden (*B. smithi*), and Atlantic Menhaden (*B. tyrannus*) collected throughout the Gulf of Mexico in 2002–04. Statistics were determined with Arlequin, vers. 3.5 (Excoffier et al., 2005). Statistics include the number of alleles, expected heterozygosity (H_e), and proportion of simulations that resulted in a more extreme test statistic for the Hardy-Weinberg equilibrium (HWE) exact test within samples (equivalent to an exact P-value). Statistical significance of the HWE *P*-value (initial α=0.05) was determined before (*) and after (**) sequential Bonferroni adjustment.

	Finescale Menhaden			Yellowfin Menhaden			Atlantic Menhaden		
	Alleles	H_e	HWE	Alleles	H_e	HWE	Alleles	H_e	HWE
Bp003	2	0.130	1.000	1	0.000	na	10	0.546	0.622
Bp017	2	0.426	1.000	2	0.193	1.000	8	0.640	0.073
Bp039	4	0.133	0.065	1	0.000	na	5	0.625	0.370
Bp121	8	0.719	0.341	5	0.700	0.190	12	0.825	0.512
Bp155	0	0.000	na	0	0.000	na	0	0.000	na
Bp221	5	0.575	0.318	3	0.323	0.489	9	0.611	0.363
Bp230	7	0.769	0.787	7	0.693	0.810	9	0.838	0.000**
Bp239	9	0.862	0.052	7	0.660	0.696	17	0.927	0.009*
Bp275	6	0.662	0.091	3	0.398	1.000	14	0.890	0.056
Bp301	8	0.779	0.286	10	0.848	0.028*	11	0.866	0.010*
Bp473	2	0.130	1.000	3	0.479	0.720	4	0.363	0.118
Bp489	2	0.045	1.000	1	0.000	na	1	0.000	na
Bp500	5	0.355	0.201	1	0.000	na	11	0.813	0.034*
Bp531	5	0.593	0.335	5	0.599	0.386	11	0.889	0.900
AF039657	2	0.045	1.000	2	0.053	1.000	12	0.698	0.231
AF039658	8	0.791	0.195	5	0.679	0.199	11	0.837	0.000**
AF039660	3	0.519	0.000**	3	0.280	1.000	4	0.550	0.000**
AF039661	1	0.000	na	2	0.341	1.000	2	0.068	1.000
AF049462	9	0.804	0.620	7	0.707	0.148	19	0.937	0.004*
Overall	4.6	0.439	–	3.6	0.366	–	8.9	0.628	–

high values of F_{is}; of these, 4 loci also indicated low frequency (p_n<0.10) null alleles. The Mantel test indicated a lack of correlation between genetic divergence and geographic distance (Mantel r=0.415, P=0.131).

Discussion

The analysis of population structure in wild species can be confounded by a paucity of readily available marker loci that are designed for a specific genus or species. The genus *Brevoortia* is one in which previous studies have been hindered by loci that lacked adequate genetic variability (Anderson, 2007; Anderson and Karel, 2007; although, see Lynch et al., 2010). The stated purpose of this study was to develop more effective tools for genetic analysis of *Brevoortia* spp. that could be used in the context of stock assessments. In particular, the intended purpose of the additional loci was 1) to improve the stock definition of the menhaden fishery in the Gulf of Mexico as it pertains to the proportion of each menhaden species in the annual catch and 2) to determine whether multiple populations of Gulf Menhaden are exploited in the fishery. Because these 2 goals require somewhat different methods, we assessed each independently in the context of the microsatellite loci described in this study.

Species identification of individuals that occur within the Gulf of Mexico menhaden fishery can be challenging. Although there are well-described morphological differences between Gulf Menhaden, Yellowfin Menhaden, and Finescale Menhaden, differences in morphological characteristics are subtle and can potentially lead to inaccurate identification (Dahlberg, 1970; Anderson and McDonald, 2007). Genetic differentiation has been equally problematic. Anderson (2007) described reciprocal monophyletic mitochondrial DNA lineages between Gulf Menhaden and both of its congeners in the Gulf of Mexico. However, this same mtDNA analysis indicated that Finescale Menhaden and Yellowfin Menhaden could not be reliably distinguished with mtDNA.

Species identification through the use of mtDNA loci can be troublesome when closely related species are hybridizing, as is the case with Gulf Menhaden and Yellowfin Menhaden (Turner, 1969; Dahlberg, 1970; An-

Table 4

Statistics from the Whichloci analysis of 14 microsatellite loci in the genus *Brevoortia*. The average rank, locus score, relative score (the power of an individual locus for species discrimination, relative to the power of all 14 loci), and cumulative score were calculated from locus scores across 100 replicated simulations of species assignment for Gulf Menhaden (*Brevoortia patronus*), Finescale Menhaden (*B. gunteri*), or Yellowfin Menhaden (*B. smithi*). The LOD (log odds) columns indicate whether inclusion of a locus was necessary ("1") or not necessary ("0") for correct assignment at the given level of stringency.

Locus	Avg. rank	Score	Relative score (%)	Cumulative score	LOD=2	LOD=3	LOD=4
AF039657	1	0.938	18.45	18.45	1	1	1
Bp500	2	0.900	17.70	36.15	1	1	1
Bp473	3	0.763	15.00	51.14	1	1	1
Bp531	4	0.701	13.79	64.93	0	1	1
AF049462	5	0.384	7.54	72.48	0	1	1
Bp489	6	0.324	6.38	78.85	0	1	1
Bp003	7	0.252	4.95	83.80	0	0	1
Bp039	8	0.238	4.67	88.48	0	0	1
Bp121	9	0.209	4.11	92.59	0	0	1
Bp221	10	0.183	3.60	96.18	0	0	1
Bp239	11	0.117	2.30	98.48	0	0	1
Bp275	12	0.071	1.39	99.88	0	0	1
AF039658	13	0.006	0.12	100.00	0	0	1
Bp230	14	0.000	0.00	100.00	0	0	1

derson and Karel, 2007) and potentially could be the case with Gulf Menhaden and Finescale Menhaden (Anderson and McDonald, 2007). In the case of hybrids of Gulf Menhaden and Yellowfin Menhaden, F1 individuals usually carry the mtDNA haplotype of Yellowfin Menhaden. Assuming that hybridization is common in the eastern Gulf of Mexico, mtDNA species identification potentially would lead to overestimation of the presence of Yellowfin Menhaden in catch data if hybrid populations are encountered because hybrids would be identified incorrectly as pure Yellowfin Menhaden. Hybrids were not encountered in our current study; however, to obtain individuals of unequivocal taxonomic classification, sampling was directed toward locales where hybridization had not previously been observed.

The uncertainty in mtDNA monophyly among *Brevoortia* species led Lynch et al. (2010) to question the taxonomic validity of Gulf Menhaden and Atlantic Menhaden. Given this uncertainty, species identification in these species by DNA analysis would be accomplished most reliably with multiple co-dominant loci. The analysis of Anderson and Karel (2007) indicated that species identification in the presence of hybrids could be achieved with as few as 5 microsatellites, although there was some uncertainty in estimation of levels of introgression in hybrid individuals.

In our study, the 14 loci used in simulated species-identification analysis (Powsim analysis) included not only 3 of the loci used in Anderson and Karel (2007) but also an additional 11 loci, some of which performed at least as well in species identification as the original loci. The Whichloci analysis indicated that the 6 most informative loci in this group could be used to distinguish between Gulf Menhaden, Yellowfin Menhaden, and Finescale Menhaden with 100% accuracy, and with a statistical error rate of α=0.001. Accuracy in species identification can be achieved with a statistical error rate of α=0.0001 given use of all 14 loci. These loci, therefore, represent a powerful tool in species identification, and can be used to reliably distinguish all Gulf of Mexico species (and hybrids) for the purpose of future stock enhancements.

To our knowledge, only a single previous study has attempted to explicitly examine the genetic structure of Gulf Menhaden in the Gulf of Mexico with intensive sampling.[3] This earlier study was conducted with 5 microsatellite loci and a single mtDNA locus; the Powsim analysis used here indicates that this level of genetic sampling is inadequate to answer questions about fine-scale population structure in this species. Success in assignment of individuals to populations is a function of both the number of loci used and the polymorphism (number of alleles) at each locus (Bernatchez and Duchesne, 2000). The loci described here improve both of those aspects of population assignment and represent a significant improvement in the tools available

[3] Anderson, J. D. 2006. Conservation genetics of Gulf Menhaden (Brevoortia patronus): implications for the management of a critical forage component for Texas coastal gamefish ecology. Federal Aid in Sportfish Restoration Act Technical Series, F-144-R, 34 pp.

to managers in assessment of population structure in the Gulf Menhaden. An analysis of genetic structure in Gulf Menhaden using these loci showed no evidence for discreet populations and no evidence for isolation-by-distance across a majority of the range of the species in the northern Gulf of Mexico. It has long been suspected that genetic divergence among Gulf Menhaden samples throughout the Gulf of Mexico is very low, and, therefore, stock assessments have generally assumed that the menhaden fishery in the Gulf of Mexico is centered upon a single fishery stock. Although the results of this study are a compelling validation of that assumption, the small sample sizes examined here relegate this finding as preliminary rather than conclusive. The power analysis indicated that sample sizes of 50 or more are necessary to conclusively detect very low levels of genetic divergence (F_{st} ≤0.004) through the use of all 15 markers for Gulf Menhaden.

Although the loci described in this article are polymorphic in other species of *Brevoortia*, the power of these markers for fine-scale population assessments in these species was not rigorously tested. The polymorphism exhibited by samples of Gulf Menhaden at these loci was not repeated to the same magnitude in other congeners. The finding that other *Brevoortia* species exhibit relatively low genetic variation at loci originally discovered in Gulf Menhaden is not surprising. Ascertainment bias, or decreased genetic variability in species that were not directly targeted in the original marker selection process, is a common finding in genetic studies of microsatellite loci among closely related species (Ellegren et al., 1997: Hutter et al., 1998; Vowles and Amos, 2005). Both heterozygosity and PIC scores were lower in all 3 *Brevoortia* congeners.

The ascertainment biases in comparisons that involve Gulf Menhaden and either Finescale Menhaden or Yellowfin Menhaden were more profound than were the biases in comparisons between Gulf Menhaden and Atlantic Menhaden. In the former 2 comparisons, there were qualitative differences in the median PCR fragment lengths in direct comparisons of species (Gulf Menhaden generally had longer alleles) and significantly higher genetic variability in the focal species (Gulf Menhaden exhibited higher PIC and H_e). In contrast, PCR fragment lengths were generally similar between Gulf Menhaden and Atlantic Menhaden, although there was a significant difference in H_e and PIC. Similar median repeat lengths between Gulf Menhaden and Atlantic Menhaden likely reflect a shallow evolutionary lineage between these species (Bowen and Avise, 1990; Anderson, 2007), in contrast to relatively deep taxonomic divergence between Gulf Menhaden and both Yellowfin Menhaden and Finescale Menhaden (Anderson, 2007). This result not only underscores the notion that the loci described here will be useful in future studies of both Gulf Menhaden and Atlantic Menhaden but also indicates that the use of loci in studies of Yellowfin Menhaden and Finescale Menhaden should be undertaken with caution.

Conclusions

It has been suggested previously that the main species exploited in the menhaden fishery of the Gulf of Mexico is the Gulf Menhaden (Ahrenholz, 1981). Because of the importance of this fishery in the Gulf of Mexico and because of the significance of Gulf Menhaden to inshore trophic systems, this finding should be re-assessed. In particular, the proportional contribution of each menhaden species occurring in the Gulf of Mexico to the annual catch should be examined through the use of a systematic method. Moreover, the presence of a single population of Gulf Menhaden throughout the Gulf of Mexico has been assumed in recent stock assessments, although this assumption has not been rigorously tested. The species composition and the number of exploited Gulf Menhaden populations can be reliably assessed with genetic data. The gene loci described in this study can be used to address both of these concerns, and they represent an improvement in the tools available for examination of the population structure of the genus Brevoortia.

Acknowledgments

This work was funded by the Texas Parks and Wildlife Department, Coastal Fisheries Division (TPWD-CF). We wish to thank D. McDonald for helpful comments on the first draft. An internal TPWD-CF review was conducted by M. Fisher and 3 anonymous reviewers. Reference to trade names does not imply endorsement by the state of Texas.

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Home range and seasonal movements of Black Sea Bass (*Centropristis striata*) during their inshore residency at a reef in the mid-Atlantic Bight

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Abstract—Black Sea Bass (*Centropristis striata*) in the mid-Atlantic Bight undertake seasonal cross-shelf movements to occupy inshore rocky reefs and hardbottom habitats between spring and fall. Shelf-wide migrations of this stock are well documented, but movements and home ranges of fish during their inshore residency period have not been described. We tagged 122 Black Sea Bass with acoustic transmitters at a mid-Atlantic reef to estimate home-range size and factors that influence movements (>400 m) at a 46.1-km^2 study site between May and November 2003. Activity of Black Sea Bass was greatest and most consistent during summer but declined rapidly in September as water temperatures at the bottom of the seafloor increased on the inner shelf. Black Sea Bass maintained relatively large home ranges that were fish-size invariant but highly variable (13.7–736.4 ha), underscoring the importance of large sample sizes in examination of population-level characteristics of mobile species with complex social interactions. On the basis of observed variations in movement patterns and the size of home ranges, we postulate the existence of groups of conspecifics that exhibit similar space-use behaviors. The group of males released earlier in the tagging period used larger home ranges than the group of males released later in our study. In addition, mean activity levels and the probability of movement among acoustic stations varied among groups of fish in a complex manner that depended on sex. These differences in movement behaviors may increase the vulnerability of male fish to passive fishing gears, further exacerbating variation in exploitation rates for this species among reefs.

Manuscript submitted 21 January 2013.
Manuscript accepted 11 December 2013.
Fish. Bull 112:82–97 (2014).
doi: 10.7755/FB.112.1.5

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necesarily reflect the position of the National Marine Fisheries Service, NOAA.

The vulnerability of marine and estuarine species to capture by recreational and commercial fisheries is enhanced when individuals aggregate during a predictable time of year. For example, the spring spawning migrations of anadromous fishes, such as American Shad (*Alosa sapidissima*) and Striped Bass (*Morone saxatilis*), historically fueled productive fisheries along the U.S. Atlantic coast (Limburg and Waldman, 2009). In the mid-Atlantic region, fishes that use inshore reefs as feeding and spawning areas between spring and fall also may increase their vulnerability to fishing gear because individuals are associated with well-defined habitat features that may be targeted by fishing operations.

Management of species that exhibit aggregation behaviors often is dependent upon spatially explicit regulations that aim to protect differentially vulnerable individuals. For instance, the harvest of blue crabs is prohibited in the lower Chesapeake Bay and the adjacent coastal ocean from May through mid-September to protect spawning females (Miller et al., 2011[1]). Similarly, marine protected areas and reserves may be used to reduce or eliminate fishing mortality on depleted stocks (e.g., the sea scallop fishery in the North Atlantic; Murawski et al., 2000). For such area closures and related spatial management approaches, many of the individuals from the target population area are assumed to use protected areas and their movements away from these areas are assumed to be minimal and temporary. Therefore, to achieve management goals, protected areas or networks of reserves should be large enough to sufficiently encompass the home ranges of individuals of the target populations (Moffitt et al., 2009).

Home range and movements of mobile species can be assessed with acoustic telemetry (e.g., Dawson and Starr, 2009; Douglas et al., 2009; Meyer et al., 2009; Farmer and Ault, 2011; Knip et al., 2012). Although such techniques provide temporally

[1] Miller, T. J., M. J. Wilberg, A. R. Colton, G. R. Davis, A. Sharov, R. N. Lipcius, G. M. Ralph, E. G. Johnson, and A. G. Kaufman. 2011. Stock assessment of the blue crab in Chesapeake Bay. Univ. Maryland Center for Environmental Science, Technical Report Series TS-614-11, 203 p. [Available at http://www.cio.noaa.gov/Policy_Programs/prplans/ID180_Chesapeake_Blue_Crab_Assessment.document_final_approved.pdf.]

intensive information, many acoustic studies of the home ranges of fishes have been conducted on relatively small spatial scales (hundreds of meters to a few kilometers) or during brief periods of time (days to weeks) with few fish (typically 15 or less). These spatial and temporal scales of study may be sufficient for elucidating the size of the home range of relatively sedentary fishes that inhabit restricted areas, such as coral reefs. However, recent work indicates that estimates of home range may be larger when habitat use of a target fish is monitored over larger spatial scales and over longer time periods (Farmer and Ault, 2011). Furthermore, because movement behaviors may vary among individuals, large sample sizes could improve our understanding of the size of the home range for a given species.

Predictable seasonal aggregations of Black Sea Bass (*Centropristis striata*) occur in nearshore areas of the mid-Atlantic region. Between spring and fall, populations of this species are exploited by recreational hook-and-line fisheries, as well as by commercial pot fisheries (Shepherd and Terceiro, 1994). The Black Sea Bass is a demersal species in the family Serranidae, and individuals are commonly found to associate with hard-bottom structures, such as reefs, rock outcroppings, and wrecks (Steimle and Zetlin, 2000; Fabrizio et al., 2013). Along the Atlantic coast, individual fish undertake annual migrations to the middle- and outer-continental shelf during winter (Musick and Mercer, 1977; Moser and Shepherd, 2009); in the spring, Black Sea Bass migrate inshore, often returning to areas occupied in the previous year (Moser and Shepherd, 2009). Timing of these seasonal cross-shelf migrations varies with latitude, but fish movements are believed to be in response to changes in water temperature at the bottom of the seafloor and in photoperiod (Moser and Shepherd, 2009; Fabrizio et al., 2013). Black Sea Bass are protogynous hermaphrodites, and larger fish (>450 mm total length [TL]) tend to be predominantly male (NEFSC[2]). During the spawning season, mature (dominant) males can be identified by a bright blue hump on the nape. However, external morphological differentiation among subordinate males, transitional males, and females is not possible for this species (NEFSC[2]). Because harvests are directed at larger fish (>250 mm TL), mature males tend to experience higher fishing-induced mortality rates than females and less developed males.

Spatial regulations are not used currently to manage Black Sea Bass, but a coastwide tagging study has indicated that exploitation rates among individual reefs in the mid-Atlantic region may be highly variable (NEFSC[3]). Furthermore, because Black Sea Bass spawn in summer while resident at these reefs (Musick and Mercer, 1977), the effect of localized fishing on the future production of this stock is unknown. Moser and Shepherd (2009) indicate that the individuals of the mid-Atlantic stock off the coast of New Jersey are fairly sedentary while resident in inshore waters; because they inferred these movements from a conventional tagging study, movements that occurred between the time of capture and subsequent recapture could not be discerned. Data from conventional tagging studies cannot be used to resolve movements at fine temporal scales (e.g., hours to days), although it is known that many fishes display regular activity patterns that may change seasonally (Reebs, 2002).

In this study, we used acoustic tagging to investigate the home range and seasonal movements of Black Sea Bass during their inshore residency at a temperate reef in the mid-Atlantic Bight. We examined the effect of fish size, sex, and duration of occupancy on size of home ranges, and we explored the effects of sex and time on movement and activity levels of individual fish. We considered a range of temporal scales, from diel to those occurring over several months, to describe movements of fish on the reef.

Materials and methods

Study site and acoustic grid

We established a 46.1-km^2 grid that consisted of 72 moored receivers (model VR2, Vemco, Ltd.,[4] Bedford, Nova Scotia, Canada) at 72 acoustic stations within a study site about 6.5 km off the coast of New Jersey (Fig. 1, A and B). In April 2003, adjacent receivers were placed 800 m apart because a range test conducted earlier at this site indicated that the effective detection range of deployed receivers was about 400 m (Fabrizio et al., 2013). Sediments at this site ranged from fine-grain mud to coarse-grain material, such as sand, gravel, and rocks (Lathrop et al., 2006); rock outcrops were observed near the center of this site (Butman[5]). Historically, this area comprised a number of "dump sites" used to dispose of dredged materials from the Port of New York and New Jersey, as well as of construction material and other refuse. In 1997, the 53.8-km^2 area that surrounds the old dump sites was designated a Historic Area Remediation Site (HARS). This site is used by Black Sea Bass during their inshore residency

[2] NEFSC (Northeast Fisheries Science Center). 2012. 53rd northeast regional stock assessment workshop (53rdSAW) assessment report. Northeast Fish. Sci. Cent. Ref. Doc. 12-05, 559 p. [Available from National Marine Fisheries Service, 166 Water St., Woods Hole, MA 02543-1026.

[3] NEFSC (Northeast Fisheries Science Center). 2004. 39th northeast regional stock assessment workshop (39th SAW) assessment summary report. Northeast Fish. Sci. Cent. Ref. Doc. 04-10a, 16 p. [Available from National Marine Fisheries Service, 166 Water St., Woods Hole, MA 02543-1026.]

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5] Butman, B. 2002. Mapping the seafloor of the Historic Area Remediation Site (HARS) offshore of New York City. U.S. Geological Survey Fact Sheet 001-02, 4 p. [Available at http://pubs.usgs.gov/fs/2002/fs001-02/fs001-02.pdf.]

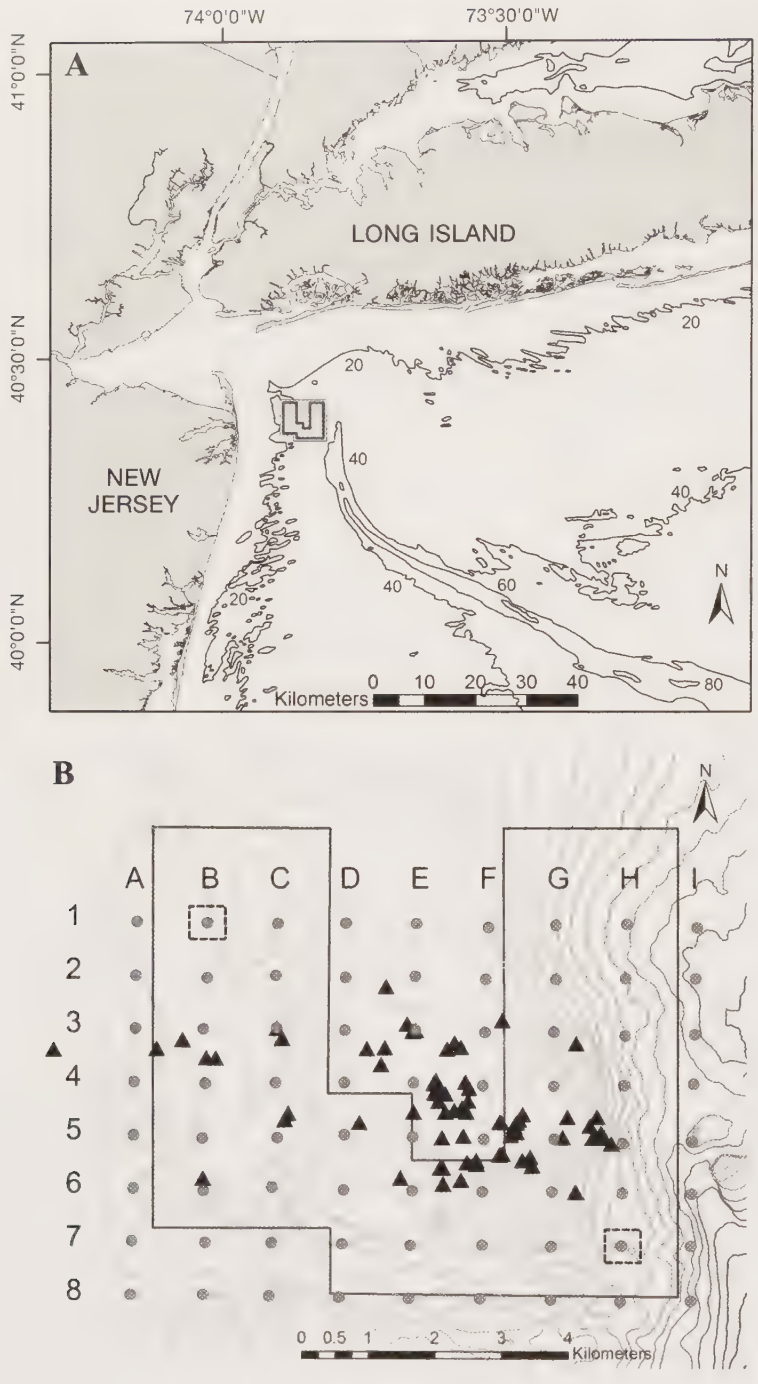

Figure 1

(**A**) Location and bathymetry (20-m isobaths) of the Historic Area Remediation Site (HARS) in the mid-Atlantic Bight. (**B**) Grid of stations where 72 acoustic receivers were deployed (filled circles) and locations where Black Sea Bass (*Centropristis striata*) were released (filled triangles) at the HARS (solid black line) between May and July 2003. The contour lines are 1-m isobaths and the acoustic grid encompasses 46.1 km^2 of the HARS. Column (A–I) and row (1–8) designations represent naming conventions for acoustic stations. Dashed squares at stations B1 and H7 indicate locations of sensors used to measure temperature and salinity at the bottom of the seafloor.

(Fabrizio et al., 2013), and this population supports recreational fisheries in New York and New Jersey.

At each acoustic station, we deployed an array that consisted of a 400-lb pyramidal anchor, an acoustic receiver (VR2), and a shallow-water release encased in a positively buoyant canister (SWR Pop-Up recovery system, ORE Offshore, West Wareham, MA). To provide maximum horizontal sensitivity (Clements et al., 2005), receivers were oriented vertically. Pop-up buoys facilitated retrieval of receivers during fall 2003 and in summer 2004. Temperature and salinity sensors (SBE 16 SeaCAT Recorder, Sea-Bird Electronics, Inc., Bellevue, WA) were deployed at stations B1 and H7 (for locations of these stations, see Fig. 1B), suspended about 3 m above the substratum; these sensors recorded data every 30 min. We used mean daily temperature, mean daily salinity, and mean daily difference in temperature and salinity between the 2 stations as measures of environmental conditions at the site. In this study, we analyzed acoustic data collected from 30 May to 14 December 2003 to estimate home ranges and describe movements of Black Sea Bass in the mid-Atlantic Bight during their inshore residency period.

Implantation of transmitters

We captured 129 Black Sea Bass at various locations within the acoustic grid at the HARS between 30 May and 16 July 2003 and implanted them with acoustic transmitters before release near the location of capture (Fig. 1B). Fish identification was made on the basis of Collette and Klein-MacPhee (2002). Black Sea Bass were captured by either hook-and-line angling (n=45) or commercial fish traps (n=84) that were allowed to soak at the site for 1–3 nights before retrieval. Upon capture, all fish were immediately placed into onboard holding tanks supplied with flow-through seawater. Although swim bladder inflation was evident in most fish, neither deflation with a hypodermic needle (Collins et al., 1999) nor "hanging" the traps at a depth of 10 m (Neufeld and Spence, 2004) completely eliminated decompression trauma. Before surgery, we anesthetized fish with 80 mg/L Aqui-S (Aqui-S New Zealand Ltd., Lower Hutt, New Zealand); this concentration allowed us to induce anesthesia in reasonably short times (mean, 3.3 min; range, 1.1–7.7 min; n=127 [induction time was not recorded for 2 fish]).

Transmitters (V8SC-2H, Vemco, Ltd., Bedford, Nova Scotia, Canada) were implanted in 129 anesthetized Black Sea Bass (mean size, 307 mm TL; range, 220–431 mm TL; n=129) at the study site using surgical techniques described in Fabrizio and Pessutti (2007). Dummy transmitters of the same size (30 mm long and 9 mm in diameter), shape, and weight (5 g in air, 3.1 g in water) had 100% retention rates in laboratory-held Black Sea Bass (Fabrizio and Pessutti, 2007). Transmitters emitted a coded acoustic signal at 69 kHz every 210 s on average (signal delay varied randomly between 120 and 300 s) and had a battery life of 384 d. Surgery time averaged 4.1 min (range, 2.0–11.7 min; n=128 [surgery time not recorded for 1 fish]); immediately after surgery, the length and sex of each fish was recorded. Sex determination was limited to classification of fish as either male (n=34) or fish of unknown sex (n=88); the latter group included females, subordinate males, and transitional males.

Sizes of the 2 groups overlapped: males ranged between 270 and 431 mm TL, with a mean of 343.5 mm TL (±standard error of the mean [SE] 6.32) and fish of unknown sex ranged between 220 and 395 mm TL, with a mean of 292.6 mm TL (SE 4.50). We used ram ventilation to resuscitate fish in a flow-through seawater tank onboard the vessel and released fish within the study site as soon as fish were able to swim forcefully downward. All procedures were conducted at a mean temperature of 17.8°C (range: 13.6–24.2°C) and 27.1 psu salinity (range: 22.1–31.0 psu). Of the 129 implanted fish, 5 carried transmitters that malfunctioned and 2 fish died within hours of release, resulting in 122 live Black Sea Bass with functioning transmitters.

Home range

Home-range area, measured in hectares (ha), was calculated for individual Black Sea Bass with the kernel density estimator. Kernel methods provide a probabilistic description of the space used by an organism and require a smoothing parameter to efficiently describe the density distribution of the individual location data (Worton, 1989). We used the bivariate normal distribution to estimate kernel home ranges with the *adehabitat* package in R (R Development Core Team, 2005; Calenge, 2006). For each fish, we eliminated observations from the release date to exclude data from the period during which fish may have been recovering from surgery and excluded data from the last week of occupancy at the site to ensure that we considered only those fish that were clearly not in the process of dispersing from the study site (Fabrizio et al., 2013); as a result, 109 fish were retained for analysis of home range.

We used the 85% probability polygon to define home-range area and investigated the effect of sex on home range through the use of an analysis of covariance with fish size, duration of occupancy (days), and release date as covariates. Duration of occupancy was estimated on the basis of the total number of days that the fish was detected within the study site, and this estimate is likely a conservative one. In particular, fish captured, tagged, and released at the end of the tagging period may have previously occupied the site.

Release date was considered in the model because preliminary investigations revealed potentially significant variation in home-range size associated with this factor. The model, which contained only fixed effects, was fitted using the MIXED procedure in SAS (vers. 9.3, SAS Institute, Inc., Cary, NC), and model parameters were estimated with restricted maximum likelihood (REML) (Littell et al., 2002). Examination of residuals from an initial model run indicated heterogeneity of variance in the home-range data; we, therefore, $\log_e$-transformed home ranges and verified that residuals from this model supported the assumption of homogeneity of variance. To test the assumption of equality of slopes for males and fish of unknown sex, we fitted a model that included all possible 2-way interactions with sex (sex×duration of occupancy, sex×length, and sex×release date):

$$Y_{ijk} = \mu + \delta + \gamma + \alpha_i + \beta_j + (\alpha\delta)_i + (\alpha\gamma)_i + (\alpha\beta)_{ij} + \varepsilon_{ijk},$$

where Y_{ijk} = the natural log of the home range for the k^{th} fish of the i^{th} sex released on the j^{th} date;
μ = the intercept;
δ = the effect of duration of occupancy (days);
γ = the effect of fish size;
α_i = the effect of the i^{th} sex;
β_j = the effect of the j^{th} release date; and
ε_{ijk} = the random unexplained error.

Indices of movement

To gauge movement of fish, we developed 2 indices. The binomial movement index allowed us to investigate factors associated with movement (e.g., are fish more likely to move during the night?), whereas the continuous activity index provided information on the extent of movements (e.g., how does activity level change in response to temperature?). The movement index indicated whether fish moved between adjacent acoustic stations during a given 3-h interval on a given day; this index was coded "0" (no movement) or "1."

To minimize autocorrelations among hourly observations, we considered location data during 4 time periods of each day: dawn, day, dusk, and night. Dawn and dusk periods were defined as the 3 hours centered on the beginning and end of nautical twilight (U.S. Naval Observatory, http://aa.usno.navy.mil/faq/docs/RST_defs.php); day and night were defined as the 3-h periods midway between dawn and dusk or dusk and dawn. The movement index for each time period was calculated daily for each fish between the time of tagging and 19 November 2003; after this date, fewer than 3 fish were detected in a given time period. In this manner, 24,789 observations from 121 fish were available

for analysis (one fish was detected at the study site for <3 h and was, therefore, excluded from analysis).

The activity index was defined as the average number of times a fish moved between adjacent acoustic stations per hour during a given 3-h time period (dawn, day, dusk, and night). This index was calculated for fish that moved at least once in a 3-h period, and values for this index ranged between 0.33 and 9. Like the movement index, the activity index indicated movements on the scale of about 400 m. Activity indices were calculated for each time period between the time of tagging and 6 November 2003 because observations on activity levels were not temporally consecutive after this date. As before, 121 fish contributed information; 11,843 observations were available for this index.

Analysis of movement

We used a generalized linear model to examine diel and seasonal patterns in fish movement and to estimate the probability that a fish moved as a function of sex, water temperature at the bottom of the seafloor, and salinity at the bottom of the seafloor. We did not consider effects of fish size because preliminary investigations indicated that movement did not vary with size. Time entered the model as continuous linear, quadratic, and cubic effects and corresponded to calendar day (i.e., time=1 on 30 May, and time=174 on 19 November). Quadratic time effects allow the direction of the response to change once (e.g., the response increases, reaches a maximum, and then decreases); cubic time effects are required when the direction of the response changes twice. All time factors were standardized to remove effects of collinearity; centering the data was not effective. The effects of season (summer [30 May–7 Sep] or fall [8 Sep–19 Nov]) and time period (dawn, day, dusk, and night) also were considered.

In addition to these multiscale temporal effects, we examined the effect of release group (defined according to tagging date: early June, late June, or July) because preliminary modeling indicated heterogeneity of movements for fish tagged at different times. Environmental effects were characterized by water temperature and salinity measured at the bottom of the seafloor at the study site. Specifically, we used mean bottom water temperature at station B1 and differences in mean water temperature and salinity at the bottom of the seafloor between stations H7 and B1; these measures were estimated for each day of the study and standardized by scaling the data with the standard deviation. These environmental factors were selected because tolerance estimates for other measures (e.g., mean temperature at station H7) indicated strong collinearity with time (tolerance values <0.10) that could not be removed through standardization or centering (Quinn and Keough, 2002).

Because movement indices (0, 1) were recorded daily for each fish during 4 time periods, we analyzed these data with a repeated-measures approach to address the potential correlation among observations from each fish. Furthermore, we identified individual fish nested within a time period as the subject for modeling the repeated measures. We fitted the following generalized linear model to the data:

$$Y_{jklmn} = \mu + \beta_j + \delta_k + \gamma_l + \lambda_m + \tau_n + \tau_n^2 + \tau_n^3 + \phi + \kappa + \alpha + interactions,$$

where Y_{jklmn} = the binomial movement index of the i^{th} fish of the j^{th} sex of the k^{th} tagging group in the l^{th} season in the m^{th} time period for the n^{th} day (time);

μ = the expected response (either 0 or 1);

b_j = the effect of the j^{th} sex;

δ_k = the effect of the k^{th} tagging group;

γ_l = the effect of the l^{th} season;

λ_m = the effect of the m^{th} time period;

τ_n, τ_n^2, and τ_n^3 = the linear, quadratic, and cubic effects of the n^{th} day;

ϕ = the effect of mean daily temperature at station B1;

κ = the effect of the mean temperature difference between stations B1 and H7;

α = the effect of the mean difference in salinity between stations B1 and H7; and

interactions refers to 2- and 3-way interactions between the fixed effects.

We did not include higher-order interactions in the generalized linear model because such complexity was either unnecessary or severely reduced the precision of the estimated parameters. In this model, Y_{jklmn} was assumed to be distributed as a binomial. The generalized estimating equation (GEE) method was used to estimate model parameters (Liang and Zeger, 1986; Littell et al., 2002) with the GENMOD procedure in SAS (vers. 9.3).

We evaluated several covariance structures to describe the potential correlation among the binomial responses: independent, compound symmetry, autoregressive with lag 1, and *m*-dependent (SAS User's Guide, vers. 9.3). For the *m*-dependent structure, correlations varied with the first *m*-time intervals, but were equal to 0 after the m^{th} interval. Because we fitted a number of potential models, we used the information-theoretic approach to identify the most suitable model from the set of models that we considered (Burnham and Anderson, 2002).

Typically, Akaike's information criterion (AIC) is calculated from model likelihoods, and differences in model values of AIC are used to guide model selection; the model with the lowest criterion is considered best. However, GEE methods do not use likelihoods to compute model parameters; instead, quasi-likelihoods are used. For GEE models, the quasi-likelihood information criterion (QIC), which is a modification of the AIC, was used to select the covariance structure that best fits the data and to guide model selection (Pan, 2004). In

keeping with this approach, we do not report *P*-values here but instead interpret the "importance" of factors on the basis of their contribution to the model.

Analysis of activity

We similarly modeled the effect of sex, time, release group, and environmental factors on the mean activity index of those fish that exhibited movement, but here we used a general linear mixed model (GLMM) fitted with the MIXED procedure in SAS (vers. 9.3; Littell et al., 2002). To meet the homogeneity-of-variance assumption, the activity index was $\log_e$ transformed. Individual fish were treated as a random factor in the model, allowing us to estimate variation among individuals. As before, we modeled the effects of the following fixed factors on the activity of fish: continuous linear, quadratic, and cubic time (standardized to eliminate collinearity), time period (dawn, day, dusk, and night), sex, season, release group, mean water temperature at station B1, and mean temperature and salinity differences between stations H7 and B1 (standardized). A repeated-measures approach was used here as well, with fish nested within time period as the subject. We used the following repeated-measures mixed model to fit the data:

$$Y_{i(m)jkln} = \mu + \alpha_{i(m)} + \beta_j + \delta_k + \gamma_l + \lambda_m + \tau_n + \tau_n^2 + \tau_n^3 + \phi + \kappa + \alpha + interactions + \varepsilon_{i(m)jklmn},$$

where $Y_{j(m)jkln}$ = the activity index of the i^{th} fish of the j^{th} sex of the k^{th} tagging group in the l^{th} season nested in the m^{th} time period of the n^{th} day (time);

μ = the expected activity index;

$\alpha_{i(m)}$ = the random effect of the i^{th} fish nested in the m^{th} time period;

interactions refers to 2- and 3-way interactions between the fixed effects;

$\varepsilon_{i(m)jklmn}$ = the random unexplained error; and other terms are as defined before.

We considered 2- and 3-way interactions in this model because such interactions greatly reduced the AIC; however, inclusion of more than two 3-way interactions or higher-order interactions resulted in severe loss of precision, and such models were abandoned. With the GLMM, we assumed that the response and the random error are normally distributed and that the variance of the response is homogeneous across the levels of the factors included in the model. We modeled heterogeneity in the covariance structure among dawn, day, dusk, and night in the GLMM through the use of the group option in the MIXED procedure and specified the Kenward-Roger method for calculating degrees of freedom (Kenward and Roger, 1997). Model building followed the approach in Zuur et al. (2007) and Bolker et al. (2008): the random structure of the model (i.e., the appropriate variance-covariance structure and the importance of the random factor) was identified with REML-based estimates of AIC. Compound symmetry, autoregressive with lag 1, autoregressive moving average with lag 1, and power covariance structures (Littell et al., 2006) were used to model the correlations among the repeated responses. Next, using the random structure identified in the previous step, we calculated AIC values for models that contained different fixed effects, using maximum likelihood; those interactions that reduced AIC values were considered important and retained. Finally, REML was used to compute the final model parameters.

Results

Acoustic data were obtained from 70 of the 72 deployed receivers and most detections occurred during the summer (from 30 May to 7 September; B4 and I2 were not recovered). After September 2003, we had reduced acoustic coverage of the study area because we were unable to retrieve 12 receivers in 2004; most of these receivers were located in areas that were infrequently occupied by Black Sea Bass (Fabrizio et al., 2013). Between 30 May and 14 December 2003, when the last detection was recorded at the site, we obtained 1,252,573 detections. Some of these detections were removed from consideration because they were redundant, occurring at the same time on adjacent receivers. Single detections, which may have resulted from acoustic or environmental interference, and occurrences of less than 5 detections during a 24-h period were also removed,[6] as were detections from unknown transmitters. Home-range and seasonal movement analyses were based on the resulting set of 1,007,787 detections.

Home range of Black Sea Bass during inshore residency

Home-range size of individual Black Sea Bass varied greatly (13.7–736.4 ha, n=109 fish), and fish of unknown sex tended to exhibit the greatest variation in home-range size (Fig. 2). About 95% of Black Sea Bass of unknown sex used areas <488.8 ha (Fig. 2; n=78). In contrast, 95% of males maintained home ranges <278.7 ha (n=31), and no males occupied home ranges >332.4 ha. On average, fish of unknown sex used 137.2 ha (SE 17.19) home ranges, and males used 120.9 ha (SE 15.29) home ranges. These mean home ranges represent about 2.6% and 2.2% of the total area of the HARS. Home ranges of individual fish overlapped.

Home-range size of Black Sea Bass varied by sex and depended on duration of occupancy (significant interaction, F=4.20, P=0.04). Using sex-specific models, we explored the effects of duration of occupancy, fish length, and release date on home ranges of males

[6] Pincock, D. G., and F. W. Voegeli. 2002. A quick course in underwater telemetry systems, 31 p. VEMCO Ltd, Bedford, Nova Scotia, Canada.

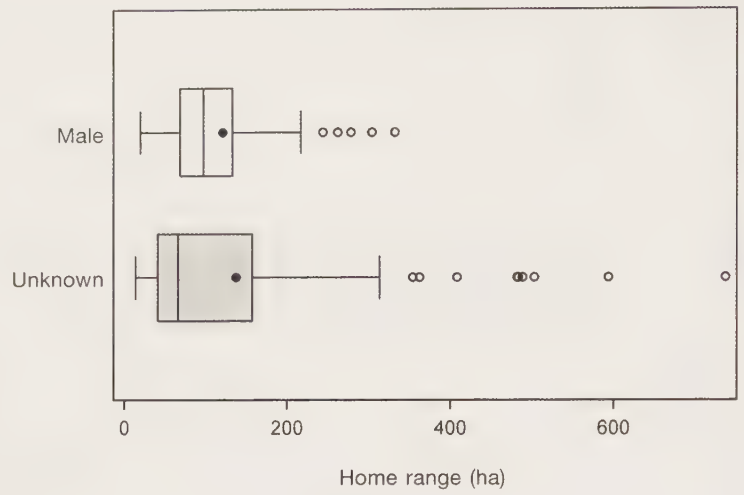

Figure 2

Distribution of home-range size (ha) of 109 Black Sea Bass (*Centropristis striata*) on the basis of 85% kernel density estimates for 31 male and 78 fish of unknown sex, a group that included females, immature males, and transitional males. Black Sea Bass were acoustically tagged and released between May and July 2003 at the Historic Area Remediation Site (Fig. 1) in the mid-Atlantic Bight. Mean home-range size is indicated by a filled circle; the vertical edges of the rectangle are the 25th and 75th percentiles; the vertical line inside the rectangle indicates the median; the whiskers extend to 1.5 times the difference between the 25th and 75th percentiles (the interquartile range); and the open circles are observations more extreme than those of the interquartile range.

and fish of unknown sex. Duration of occupancy significantly affected the home-range size of fish of unknown sex (F=14.15, P<0.01) but not the home-range size of males (F=0.01, P=0.91). Fish of unknown sex that occupied the site for short periods had significantly larger home ranges than those fish of unknown sex that occupied the site for longer periods (δ=–0.010, t=–3.78, P<0.01; Fig. 3). Duration of occupancy was the only factor that significantly affected home-range size of fish of unknown sex; neither fish size (F=0.81, P=0.37) nor release date (F=0.04, P=0.83) was significant in prediction of mean home-range size of these fish. As noted previously, estimates of the duration of occupancy may have been biased low, particularly for fish released later in the tagging period. However, release date did not affect duration of occupancy (F=0.17, P=0.69), indicating the lack of systematic bias in the estimated duration of occupancy for these fish.

In contrast to the results observed for fish of unknown sex, we found a significant effect of release date on home-range area of male fish (F=5.81, P=0.02) such that, on average, males tagged and released in early June established home ranges that were at least twice the size of home ranges established by males tagged and released in July (predicted $\text{mean}_{\text{earlyJun}}$=143.2 ha, n=7; predicted mean_{Jul}=63.0 ha, n=11; Fig. 4). Furthermore, size of male fish did not explain the observed variation in mean home range (F=0.70, P=0.41). Regardless of when male fish were tagged, the average size of these fish was similar (F=0.55, P=0.46), implying that male body size did not account for the smaller home ranges observed among fish tagged in the latter part of the tagging period.

Movement of Black Sea Bass

Black Sea Bass were more likely to move in summer than in fall; fish were also more likely to move with increasing mean daily temperature differences at stations B1 and H7. Time period did not affect the probability of movement between adjacent receivers, nor did differences across the study site in mean salinity at the bottom of the seafloor. The best model from the set of models considered was that with an m-dependent correlation structure with m=30 to model the correlations between observations; 30 time intervals corresponds to 7.5 days indicating that movement probabilities within a given week were significantly correlated, but not thereafter. The interactions retained in the model included cubic time interactions with release group and sex (and all the lower order 2-way interactions contained therein), as well as the interaction of time with mean temperature at station B1 (Table 1); these complex movement probabilities are therefore described separately for males and fish of unknown sex.

Between June and October, the probability of moving decreased for male fish and was lowest among males released in late June compared with males released at other times (Fig. 5A); between October and mid-November, the probability of moving increased for males released in July but remained low for the males released in late June (Fig. 5A). Males released in early June were no longer present at the site by mid-September; therefore, movement likelihoods could not be estimated for this group. In contrast, fish of unknown sex from all release groups exhibited similar probabilities of movement that decreased between June and November (Fig. 5B); however, fish of unknown sex released in late June maintained higher probabilities of movement between October and mid-November than did fish of unknown sex from other release groups (Fig. 5B). The most pronounced difference among the sexes occurred for the July release group between October and mid-November: among males, those fish released in July exhibited the highest probability of moving during this time period, whereas fish of unknown sex released in July exhibited the lowest probability of movement.

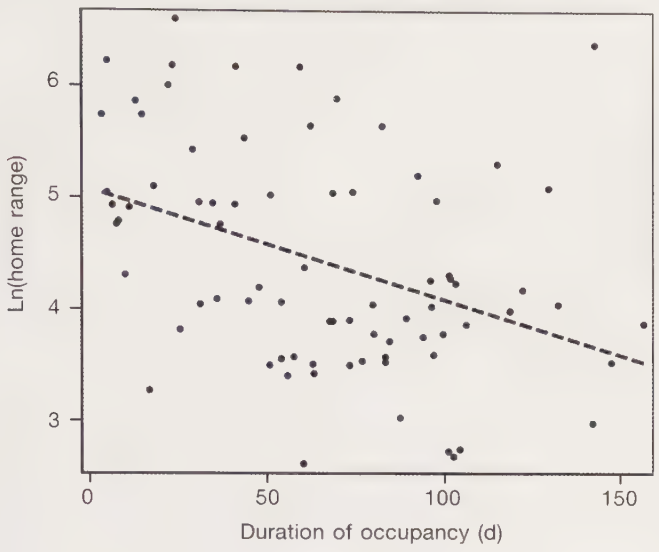

Figure 3

Relationship between $\log_e$-transformed home-range size (ha) and duration of occupancy for 78 Black Sea Bass (*Centropristis striata*) of unknown sex at a reef in the mid-Atlantic Bight during summer–fall 2003; these fish included females, subordinate males, and transitional males. Duration of occupancy was calculated as the difference between release date and date last detected at the study site in 2003; fish were released between 30 May and 16 July 2003. The dashed line is a linear regression line provided for reference only.

Linear changes in the probability of moving varied with water temperature at the bottom of the seafloor at station B1; the linear decline in the likelihood of moving was more rapid at higher water temperatures (i.e., temperatures exceeding 13°C; Fig. 6). These higher temperatures were observed at the site primarily during September. Generally, average water temperatures in fall exceeded those temperatures observed in summer: mean temperature at the bottom of the seafloor at station B1 was 15.58°C (SE 0.05) in fall and 12.60°C (SE=0.03) in summer.

Activity of Black Sea Bass

For fish that did move, the random structure of the data for the continuous activity index was best described by including the variation associated with individual fish in the GLMM and by modeling the correlations among observed movements across time periods and days with an autoregressive moving average structure (with lag 1). The difference in AIC between models with and without the random fish factor exceeded 390, indicating that an important portion of the variation in the observed continuous activity index was associated with individual fish. Variation among individuals in activity levels accounted for 22–26% of the random variation observed during any given time period (Table 2).

As we found when modeling the binomial probability of movement, activity levels of fish measured by the continuous activity index varied with season, time, release group, sex, and water temperature at the bottom of the seafloor at the study site (Table 2). Activity of Black Sea Bass decreased with decreasing differences in mean temperature across the site from summer through fall; however, the remaining main effects could not be interpreted directly because of the presence of multiple 2-way interactions (Table 2). Cubic time effects on activity of Black Sea Bass varied by season and with release group (Fig. 7) such that, during summer, fish released in early June were consistently more active than were fish released in late June or July. The mean predicted activity index exhibited less variation during summer than during fall (Fig. 7); in summer, activity levels seemed fairly constant, until about late August (day 90 in Fig. 7), when activity levels declined rapidly. Subsequently, activity levels of fish were highly variable and depended on release group: fish released in late June were more active in fall than were those fish released earlier or later (Fig. 7).

Activity levels of Black Sea Bass exhibited significant linear and quadratic changes through time in response to mean temperature but these responses differed for males and fish of unknown sex (Fig. 8). Male fish appeared less responsive to temperature than fish of unknown sex, which exhibited decreasing levels of activity with increasing temperature (Fig. 8). The effect of time period on activity of Black Sea Bass was marginal (Table 2), but our modeling results indicate that fish were slightly more active during crepuscular periods and least active during the day. Consistency of the continuous activity index during successive days was greatest at night (γ=0.3297; Table 2); these responses exhibited higher correlations across time than did responses measured during other time periods.

Discussion

Home range of Black Seas Bass during inshore residency

We provide the first estimates of home-range size for Black Sea Bass in the mid-Atlantic during their inshore residency period; individuals maintained large, overlapping home ranges (13.7–736.4 ha), reflecting the spatial extent of feeding and spawning areas. Although fish were detected throughout the study site, most fish used relatively shallow areas of coarse sediments in the central portion of the site (Fabrizio et al., 2013), indicating that the extent of suitable habitat may have restricted home ranges of these fish. Black Sea Bass that inhabit other temperate reefs in the mid-Atlantic region may exhibit larger or smaller home ranges, de-

Table 1

Comparison of the fit of the top 14 models of activity for Black Sea Bass (*Centropristis striata*) at a reef in the mid-Atlantic Bight during the period May–November 2003, with the following 10 predictors included in all models: sex; season; release group (*rg*); time period (dawn, day, dusk, and night); linear (t), quadratic (t^2) and cubic (t^3) time; mean difference in temperature at stations B1 and H7 (see Fig. 1), 2 of the stations where acoustic receivers were deployed; mean difference in salinity at stations B1 and H7; and mean temperature at station B1 (temp). The response was coded 0 (no movement) or 1 (movement) during a given 3-h time period; the subject of each repeated-measures model was individual fish nested in time period. The quasi-likelihood information criterion (QIC) is a modification of Akaike's information criterion appropriate for repeated-measures models of binomial responses.

10 Predictors +	QIC	ΔQIC
$sex*rg + sex*t^3 + rg*t^3 + temp*t + sex*rg*t^3$	32247.316	0.0
$sex*rg + sex*t^2 + rg*t^2 + temp*t^2 + sex*rg*t^2$	32265.321	18.005
$sex*rg + sex*t^3 + rg*t^3 + temp*t^3 + sex*rg*t^3$	32267.646	20.330
$sex*rg + rg*t^3 + temp*t + temp*t^2$	32277.678	30.362
$sex*rg + sex*t^3 + rg*t^3 + temp*t^2 + sex*rg*t^3$	32278.182	30.866
$sex*rg + sex*t^2 + rg*t^2 + temp*t + sex*rg*t^2$	32279.667	32.351
$sex*rg + sex*t^2 + rg*t^2 + temp*t^3 + sex*rg*t^2$	32284.446	37.130
$sex*rg + rg*t^3 + temp*t$	32284.549	37.233
$sex*rg + rg*t^2 + rg*temp + temp*t + temp*t^2 + rg*temp*t^2$	32285.540	38.224
$sex*rg + rg*t^3 + temp*t + temp*t^2 + temp*t^3$	32287.220	39.904
$sex*rg + rg*t^2 + temp*t^2$	32289.342	42.026
$sex*rg + rg*t^2 + rg*t^3 + temp*t + temp*t^2$	32293.091	45.775
$sex*rg + rg*t^3 + temp*t + temp*t^3$	32294.340	47.024
$sex*rg + rg*t^2 + temp*t$	32298.118	50.802

pending on reef size. We hypothesize that the size and spatial distribution of temperate reefs and other hardbottom structures along the Atlantic coast and in the Gulf of Mexico may contribute to observed variation in home-range size within this species.

Home-range sizes reported for other fishes tend to be relatively small (<1 ha), possibly reflecting the limited spatial and temporal scales over which these types of studies are typically conducted (e.g., Topping et al., 2005; March et al., 2010; Mason and Lowe, 2010). Additionally, fishes that exhibit a high affinity to a particular habitat (e.g., coral reefs) often have relatively small home ranges. Black Sea Bass home ranges were markedly larger than the ones reported for other structure-oriented fishes (e.g., Parrotfish [*Sparisoma cretense*]: 0.0037 ha, Afonso et al., 2008; Schoolmaster [*Lutjanus apodus*]: 4.7 ha, Gray Snapper [*L. griseus*]: 14.6 ha, Hammerschlag-Peyer and Layman, 2010). Subadult Prickly Shark (*Echinorhinus cookei*) in Monterey Canyon maintained home ranges similar in size to Black Sea Bass (20–146 ha; Dawson and Starr, 2009), as did several species of coral reef fishes in the Dry Tortugas National Park (144–417 ha; Farmer and Ault, 2011). These observations and those of

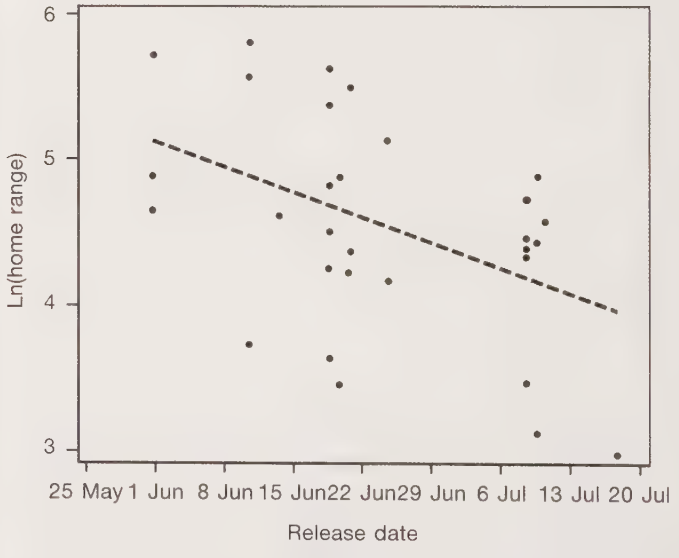

Figure 4

Relationship between $\log_e$-transformed home-range size (ha) and release date for 31 male Black Sea Bass (*Centropristis striata*) at a reef in the mid-Atlantic Bight during summer–fall 2003. The dashed line is a linear regression line provided for reference only.

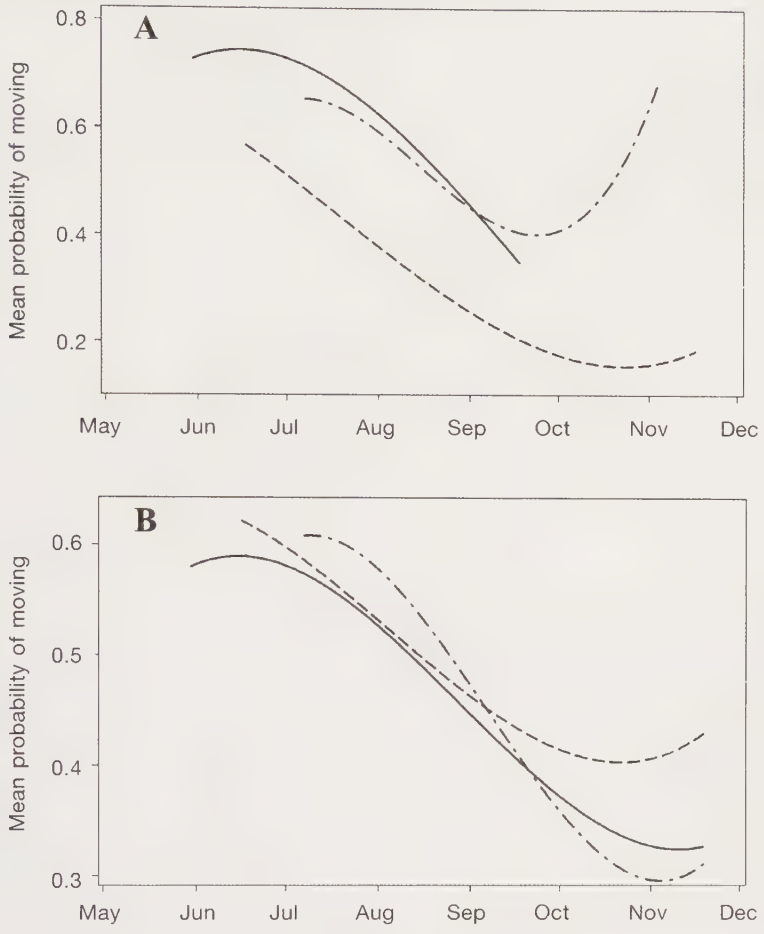

Figure 5

Effect of release group on mean predicted probability of moving for 3 groups of Black Sea Bass (*Centropristis striata*) tagged and released at a reef in the mid-Atlantic Bight in early June (solid line), late June (dashed line), and July (dotted and dashed line) 2003 for (**A**) males (n=34) and (**B**) fish of unknown sex (n=87). Movement was indexed as either 0 (no movement) or 1 (movement) and was observed from 30 May to 19 November 2003; predicted means are from a binomial repeated-measures model.

Farmer and Ault (2011) support our notion that the use of appropriate temporal and spatial domains of study is critical for estimation of home ranges of fishes.

Studies that incorporate large numbers of fish can elucidate the degree of variation in home-range sizes and may be helpful in clarifying habitat use among groups of conspecifics. We found an order of magnitude difference in home-range sizes among 109 Black Sea Bass at our study site (13.7–736.4 ha). However, the magnitude of this variation was not unusual, as Spot-tail Shark (*Carcharhinus sorrah*) in Australia used areas varying between 1 and 7802 ha as home ranges (Knip et al., 2012), and home ranges of California Sheephead (*Semicossyphus pulcher*), another protogynous hermaphrodite, spanned 2 orders of magnitude (Topping et al., 2005). The large variation in home-range size among Black Sea Bass may reflect the distribution of prey resources at the study site or the extent of competitive interactions among fish for prey and shelter. Population density at the reef also may play a role in structuring space use among conspecifics. Our study was conducted during the inshore residency period of Black Sea Bass in a single year, and, as such, the specific home-range sizes we report here may be indicative of conditions in 2003. However, the relative home-range size and order-of-magnitude variation in home ranges in this population are likely to be independent of year of observation.

Home ranges of adult Black Sea Bass were fish-size invariant. Theory indicates that larger fish may require larger areas for feeding and that larger fish are able to patrol and defend larger areas with less metabolic cost than smaller fish are able to do (Kramer and Chapman, 1999). Although such relationships have been observed in some marine fishes (e.g., Jones, 2007; Taylor et al., 2007; Marshell et al., 2011), others have reported no effect of fish size on home-range size (e.g., Lowe et al., 2003; Afonso et al., 2008; Bellquist et al., 2008; Farmer and Ault, 2011; this study). Apparent inconsistencies with theoretical expectations may arise because the relationship between body size and home-range size applies only to comparisons among species or among life stages of a given species (e.g., Jones, 2007). For example, juvenile Black Sea Bass displayed restricted use of estuarine habitats in New Jersey, rarely moving more than 120 m (Able and Hales, 1997); this geographic scale of habitat use contrasts markedly with the extent of the area used by adults during their inshore residency (this study) or throughout their life (Moser and Shepherd, 2009). However, within a given life stage of a single species, home range appears to be less affected by fish size.

Home ranges of Black Sea Bass of unknown sex (females, subordinate males, and transitional males) were smaller among individuals with longer inshore residency times, indicating that fish of unknown sex that occupied smaller home ranges (<137.2 ha) exhibited higher site affinities. These tendencies may reflect the reproductive strategy of females and small males in this group. For example, females that occupied the site for only short periods (<50 d) may move freely

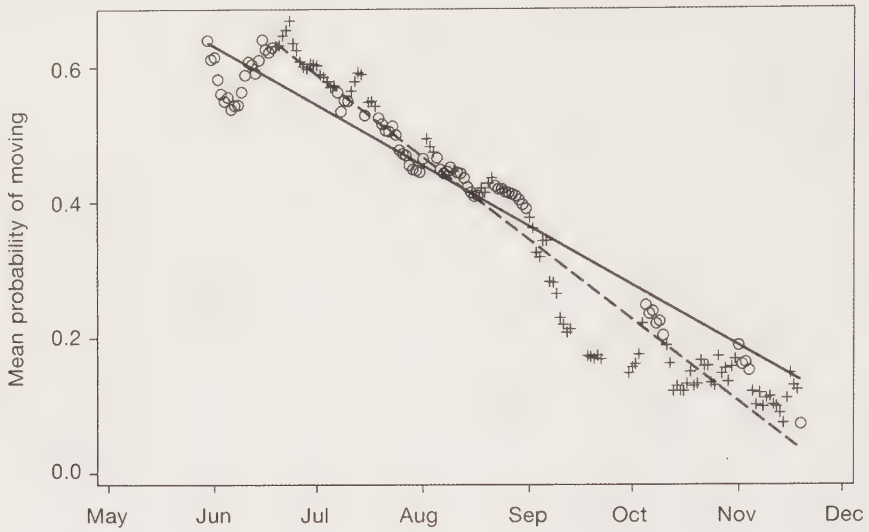

Figure 6

Mean predicted probability of moving for Black Sea Bass (*Centropristis striata*) at a reef in the mid-Atlantic Bight during periods of low (open circles, solid line) and high (crosses, dashed line) water temperatures at the bottom of the seafloor; temperatures <13°C are low, and those temperatures >13°C are high. Predictions are for 121 Black Sea Bass fitted with acoustic transmitters and tracked between late May and mid-November 2003.

among social groups (and, therefore, exhibited larger home ranges [>100 ha]), but females that occupied the site for longer durations (>100 d) may have been more strongly associated with a specific group (and, therefore, exhibited smaller home ranges [<60 ha]). The mating system of Black Sea Bass has not been observed in the wild, but on the basis of observations with captive fish (Nelson[7]), these social groups are likely to be harems. Some of the fish that exhibited larger home ranges may have been fish undergoing transformation to males (see, e.g., Mercer, 1978). As such, these fish may display exploratory behaviors, searching for territories or joining spawning groups as "sneaker" males. Additional studies on the reproductive strategies and social behavior of this species are needed to understand the mating system of Black Sea Bass and the role of sex-transitioning fish.

On average, mature male Black Sea Bass exhibited smaller home ranges than did females and subordinate or transitional males, perhaps, because mature males establish territories only as large as they can successfully patrol and defend. These sex-related differences in home-range size were similarly observed in another protogynous serranid, *Pseudanthias squamipinnis* (Shapiro, 1987). However, our study and that of Shapiro (1987) contrast with results reported for other territorial protogynous fishes, such as hogfishes (*Bodianus* spp.), for which home ranges of males exceeded those of females (Hoffman, 1983). The difference we observed for Black Sea Bass may be due to the significantly larger home ranges (13.7–736.4 ha) of fish on inner-shelf habitats compared with those of fish using coral-reef habitats, where home ranges are typically on the order of a few hundred square meters (0.01–0.05 ha; see e.g., Hoffman, 1983).

Furthermore, if we assume that fish tagged and released at a given time represented the population of available fish, then fish released early in the study may have arrived at the site earlier than those fish tagged and released later in the study period. Under this assumption, mature male Black Sea Bass that arrived early at the site (i.e., fish released in early June) established larger home ranges (>120 ha) than males arriving later in summer (fish released in July), indicating that spawning territories may be limited on the inner continental shelf and that late-arriving males may be less likely to establish and maintain larger territories.

The observed relationship between mean size of the home-range area of males and timing of release also was observed among the minimum and maximum size of the home-range area of these fish and the timing of their release. Whether home-range size is related to spawning success of males is unknown, but such knowledge could shed light on the importance of the timing of inshore migrations and the ability of males to

[7] Nelson, D. 2005. Personal commun. NOAA Fisheries Service, Northeast Fisheries Science Center, Milford, CT 06460.

Table 2

Estimated parameters from the general linear mixed model of activity level for Black Sea Bass (*Centropristis striata*) at a reef in the mid-Atlantic Bight during the period May–November 2003, with the activity index $\log_e$ transformed to meet homogeneity of variance assumptions. The model was fitted to 11,843 observations from 121 Black Sea Bass. The additional variance associated with individual fish was 0.1578; the correlations among activity levels during dawn, day, dusk, and night were modeled with an autoregressive moving average model with parameters σ^2, ρ, and Γ, where σ^2 is the estimate of the residual variance for each time period, Γ is the estimated correlation between 2 successive repeated measures, $\Gamma\rho$ is the estimated correlation between observations 2 (time) units apart, $\Gamma\rho^2$ is the estimated correlation between observations 3 (time) units apart, and so forth. Temp is temperature in degrees Celsius (°C) at the bottom of the seafloor; B1 refers to the acoustic station depicted in Figure 1; time period refers to dawn, day, dusk, and night; df is degrees of freedom.

Covariance parameter	Dawn	Day	Dusk	Night
σ^2	0.4840	0.5548	0.4637	0.4530
ρ	0.8351	0.8619	0.8636	0.7622
Γ	0.2332	0.2533	0.2603	0.3297

Type-III tests of fixed effects

Effect	Numerator df	Denominator df	*F*	*P*
Sex	1	116	0.90	0.345
Season	1	7062	0.38	0.536
Release group	2	118	1.06	0.350
Time period	3	431	1.96	0.120
Time	1	2829	96.88	<0.001
Time^2	1	5366	8.45	0.004
Time^3	1	4244	47.76	<0.001
Temp difference	1	8431	7.23	0.007
Temp at B1	1	5713	19.06	<0.001
Salinity difference	1	6163	1.54	0.215
Temp at B1*time	1	5144	9.53	0.002
Temp at B1*time^2	1	6003	22.83	<0.001
Temp at B1*sex	1	4797	34.06	<0.001
Season*time^3	1	5825	28.52	<0.001
Release group*time^3	2	3809	19.67	<0.001

successfully establish territories for reproduction and recruitment.

The observed variations in home-range size among Black Sea Bass have implications for management of these fisheries. In the mid-Atlantic, commercial and recreational fisheries target fish at specific reefs; although the distribution of fishing activity at the reefs is not strictly random, vulnerability to capture is likely to increase with increasing home-range size. The largest home ranges were observed for fish of unknown sex that occupied the site for shorter (<50 d) periods of time; occupancy duration may have been short because these fish dispersed from the site or because they were harvested or died of natural causes. Males released in early June had home-range areas that were larger than those areas of other males, indicating that groups of males may be differentially vulnerable to capture. Because reefs may support populations characterized by groups of fish that exhibit differences in space use and activity levels, differential vulnerability of groups may further exacerbate variation in exploitation rates among reefs. In addition, fishery removal of mature males may initiate sex transformation in females (Benton and Berlinsky, 2006), a process that is ensured by social interactions among individuals with overlapping home ranges.

Seasonal movements of Black Sea Bass

During their inshore residency in the mid-Atlantic Bight, Black Sea Bass were more likely to undertake large-scale movements (>400 m) during summer, when mean cross-shelf differences in water temperature at the bottom of the seafloor were more pronounced than

in other seasons. Similarly, mean activity levels of Black Sea Bass were highest during summer and declined significantly in the fall, regardless of time of day. Throughout the summer, fish maintained high mean activity levels that were fairly constant.

Seasonal declines in activity of Black Sea Bass also were observed among 14 Black Sea Bass held in captivity from July through December of 2002 in a 121,000-L research aquarium. In these captive fish, aggressive behaviors were highest soon after dominant males established territories in summer, and these behaviors declined over time.[8] Our field-based observations of lower mean activity indices in the fall are consistent with a decline in aggressive pursuits and establishment of stable territories. Although laboratory and field experiments yielded analogous results, the spatial scales of these studies were vastly different. Additional studies at the scale investigated at the HARS but with the ability to identify specific movement behaviors (e.g., foraging, evasion, searching) are necessary to determine the nature of seasonal changes in activity levels of Black Sea Bass.

Among Black Sea Bass in the mid-Atlantic, the probability of undertaking seasonal movements on the order of 400 m varied among groups of fish and depended on sex and other factors. For example, on the basis of the binomial movement index, we observed that mature males that remained at the study site after October were more likely to move than were fish of unknown sex that were present at that time. During that time, that group of males may have been more vulnerable to capture by passive fishing gear. Similarly, differences in seasonal movements unrelated to fish size were observed among release groups of male fish (Fig. 5A). On the basis of our observations, we postulate that Black Sea Bass arrive and establish residence at mid-Atlantic reefs throughout the summer; furthermore, groups of fish within these resident populations exhibit diverse seasonal movement patterns. Variations in movement patterns within a population are not likely to be the result of random movements among individuals; instead, such variations have been postulated to represent behavioral differences that may contribute to niche specializations (Hammerschlag-Peyer and Layman, 2010). Further research is necessary to elucidate factors that contribute to the formation and maintenance of behavioral groups in Black Sea Bass, including factors associated with the complex social behaviors exhibited by this species.

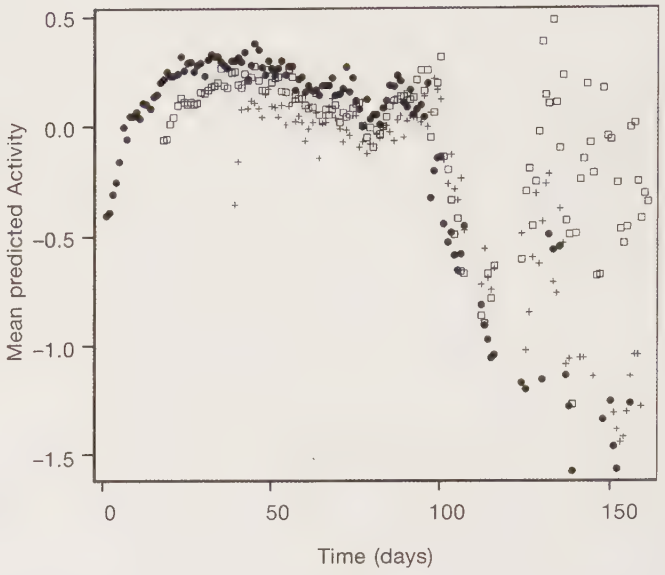

Figure 7

Mean predicted activity levels from the generalized linear mixed model for 3 groups of Black Sea Bass (*Centropristis striata*) released at a reef in the mid-Atlantic Bight in early June (filled circles), late June (squares), and July (crosses); the activity index is presented in $\log_e$-transformed units and the data span the period from 30 May (time=0) to 6 November (time=161) 2003.

Diel activity of Black Sea Bass

In some species, activity patterns are associated with environmental light levels (Løkkeborg et al., 2000) and may be mediated by temperature (e.g., Hurst and Duffy, 2005), nutritional state (Metcalfe et al., 1998), or other factors (Reebs, 2002). We observed declining activity levels (number of times a fish moved >400 m during a 3-h period) of Black Sea Bass as temperature differences across the study site decreased. However, individual fish exhibited highly variable activity levels (as measured by the continuous activity index) that were not explained by factors we considered in this study, indicating that age, physiological condition, social status, or other individual-based characteristics mediated activity levels. Additionally, interspecific interactions and the distribution and availability of prey resources likely contributed to observed variations in activity.

Differences in activity levels of Black Sea Bass during crepuscular, daytime, or nighttime periods were less striking than during different seasons. The mean activity index observed during the daytime tended to be lower than mean indices observed during crepuscular periods or at night. Black Sea Bass, which are visual feeders, feed during daylight (Steimle and Figley, 1996), and low activity levels at this time may indicate that fish feeding areas may be located near (~400 m) areas

[8] Fabrizio, M. C., J. P. Pessutti, J. P. Manderson, A. F. Drohan, and B. A. Phelan. 2005. Use of the Historic Area Remediation Site by black sea bass and summer flounder. Northeast Fish. Sci. Cent. Ref. Doc. 05-06, 95 p. [Available from National Marine Fisheries Service, 166 Water St., Woods Hole, MA 02543-1026.]

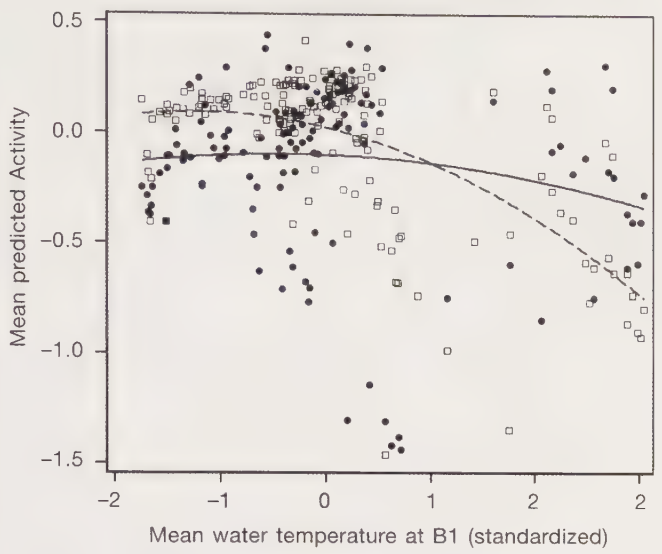

Figure 8

Mean predicted activity levels from the generalized linear mixed model for male Black Sea Bass (*Centropristis striata*) (filled circles, solid line) and fish of unknown sex (squares, dashed line) at a reef in the mid-Atlantic Bight; the activity index is presented in $\log_e$-transformed units. Mean daily water temperature at the bottom of the seafloor was measured in degrees Celsius at acoustic station B1 (see Fig. 1B) from 30 May to 6 November 2003 and was standardized to a mean of 0. Quadratic regression lines are shown for reference only.

frequented by fish during the day and that movements to and from feeding areas are not far ranging. Although adult Black Sea Bass use reefs for shelter, they do not depend exclusively on reef fauna for prey (Steimle and Figley, 1996). In New Jersey coastal waters, Black Sea Bass primarily consume juvenile Atlantic rock crabs (*Cancer irroratus*) and other invertebrates typically associated with nearby sandy sediments (Steimle and Figley, 1996; Murdy et al., 1997).

Across successive days, we observed greater consistency in mean activity levels at night than during any other time of the diurnal period. Black Sea Bass are believed to spawn at night (McGovern et al., 2002), and, at the study site, movements during night were less variable than movements observed during other times of the day. Consistent nightly activity levels of Black Sea Bass at the study site indicate that if fish spawn at night, spawning may occur near areas used for feeding and shelter. Our acoustic studies of Black Sea Bass movements and activity levels are indicative but cannot address small-scale changes in position associated with complex behaviors and interactions among individuals. For example, social hierarchies may be maintained by dominant males patrolling or defending territories and by females sampling these territories. Other approaches, such as the use of mobile acoustic telemetry or fine-scale acoustic positioning systems, are better suited for investigation of these hypotheses.

Conclusions

During their inshore residency, Black Sea Bass in the mid-Atlantic region maintained large but highly variable home ranges. Home ranges of females, subordinate males, and individuals transitioning to males depended on the duration of occupancy at the study site, whereas the home range of mature males varied with release group (i.e., groups of fish tagged in early June, late June, or July). Among these mature males, the probability of movement (>400 m) and mean activity level also varied with release group. Groups of Black Sea Bass exhibited distinct behaviors that may potentially affect growth and reproduction through effects on home-range size. Specifically, mature males released early in the study period may have arrived earlier at the inshore reef and established and maintained larger home ranges than males arriving later in summer. Our acoustic study is the first to indicate the existence of behavioral groups among wild Black Sea Bass. The use of an activity index that gauged movements on the order of 400 m revealed that Black Sea Bass were most active in summer and activity levels in other seasons were lower and more variable in comparison. Seasonal differences in activity among groups of Black Sea Bass may have resulted in differential vulnerability to exploitation by passive gears, particularly for mature males in fall. Additional studies with large numbers of fish are required to elucidate the composition of behavioral groups and the role of subordinate males, transitional males, and females in the maintenance of group behaviors.

Acknowledgments

We thank D. Mountain and M. Taylor (NOAA Fisheries, Woods Hole, MA) for loaning us the conductivity, temperature, and depth sensors and providing technical assistance and the NOAA scientists and volunteers who assisted with at-sea operations. Vessel support was provided by S. Sirois (RV *Gloria Michelle*), R. Haner (RV *Gloria Michelle*), W. Ihde (MV *Samantha Miller*), E. Christman (NOAA vessel *Thomas Jefferson*), C. Brown (RV *Nauvoo*), J. Hughes (RV *Walford*), and R. Alix (RV *Loosanoff*). We thank 2 anonymous reviewers whose suggestions helped clarify the presentation of this work. This study was funded by the U.S. Army Corps of Engineers and was conducted in accordance with guidelines concerning the use of animals in research published by the American Fisheries Society

and the American Society of Ichthyologists and Herpetologists. M. Fabrizio was partially supported by the Moses D. Nunnally fund. This article is contribution number 3333 of the Virginia Institute of Marine Science, College of William & Mary.

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Participles As adjectives, participles must modify a specific noun or pronoun and make sense with that noun or pronoun.

Incorrect: *Using the recruitment model, estimates of age-1 recruitment were determined.* [Estimates did not use the recruitment model.]

Correct: *Using the recruitment model, we determined age-1 estimates of recruitment.* [The participle now modifies the word *we,* those who were using the model.]

Incorrect: *Based on the collected data, we concluded that the mortality rate for these fish had increased.* [*We* were not based on the collected data.]

Correct: *We concluded on the basis of the collected data that the mortality rate for these fish had increased.* [Eliminate the participle and replace it with an adverbial phrase.]

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